BEHAVIORAL ECOLOGY AND POPULATION DECLINE OF THE MINK FROG, *Rana septentrionalis*

by
Michael Gunnar Tenneson

Bachelor of Arts, University of California at Los Angeles, 1980

A Thesis

Submitted to the Graduate Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the degree of

Master of Science

Grand Forks, North Dakota

December
1983

This thesis submitted by Michael Gunnar Tenneson in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

Lewis W. Chang

Diana Fuhr

Jeffrey W. Lang

John D. Williams

This thesis meets the standards for appearance and conforms to the style and format requirements of the Graduate School of the University of North Dakota, and is hereby approved.

Title BEHAVIORAL ECOLOGY AND POPULATION DECLINE OF THE MINK FROG, Rana septentrionalis

Department Biology

Degree Master of Science

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the Library of this University shall make it freely available for inspection. I further agree that permission for extensive copying for scholarly purposes may be granted by the professor who supervised my thesis work or, in his absence, by the Chairman of the Department or the Dean of the Graduate School. It is understood that any copying or publication or other use of this thesis or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my thesis.

Signature Michael D. Lannoo

Date 8 August 1983

CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would like to express my appreciation to Drs. Jeffrey Lang, John Williams, and Diana Lieberman for their constructive criticisms and review of this thesis. I owe special thanks to Dr. Lewis Oring for his time and advice concerning this project, and his painstaking review of this document. Extensive logistic support was provided by the University of Minnesota Forestry and Biological Station at Lake Itasca and by Mr. David Bosanko. I am especially thankful for the untiring assistance in the field by Alan Hodges, Erez Dror, Charlie Wellenstein, Don Price, Stacey Coffin, and my wife, Cheryl. My wife Cheryl also assisted greatly in the preparation of this thesis. Lastly I want to thank God for the help and endurance He provided me. This research was funded in part by the University of Minnesota Field Biology Program, the Minnesota Department of Natural Resources (Non-Game Program), and the University of North Dakota Graduate School.

ABSTRACT

During the summers of 1981-2, observations were made on social behavior, distribution, and abundance of the mink frog (Rana septentrionalis) in northwestern Minnesota. Six sites in Itasca State Park were used for mark-recapture studies; behavioral observations were made at a small, naturally occurring chorus (1981) and within an enclosure (1982). Playback experiments were performed at a medium-sized chorus in 1982. Captured frogs were measured, weighed and toe-clipped. In addition, subjects of behavioral studies were individually marked with waist tags.

Males chorused from late June to early August 1981-2. Because chorus activity extended for six weeks, the mink frog is classified as a "prolonged" as opposed to an "explosive" breeder (Wells 1977a).

During the breeding season, male mink frogs defended one territory containing a mean of 9.75 calling sites. Territorial males aggressively displaced intruders via overt aggression. Over half (59%) of all aggressive encounters consisted of counter-calling (alternation of vocalizations). Large males won more fights than small males. Fights consisted of jump-attacks, head-butting, wrestling, clasping, and chases.

Male reproductive success, as measured by amplexus success, was variable ($\bar{x}$= 1.3 mates, SD=4.24), and did not correlate with the physical characteristics investigated. Amplexus and oviposition were described from the wild for the first time. Because 1) the operational sex ratio was male-skewed, 2) female mink frogs appeared to oviposit within the amplexing male's territory, 3) male mink frog mating success (measured by frequency of amplexus) was variable, and 4) male mating success appeared to be related to territory quality and not characteristics of the male, the mating system of the mink frog is tentatively classified as resource defense polygyny. Female mink frogs were behaviorally cryptic and non-territorial.

The mink frog is uniquely adapted to an aquatic/ nocturnal lifestyle. Mink frog life history characteristics are compared with those of five other sympatric ranids.

Sound spectrograms (N=210) of 27 mink frogs were analyzed. Vocalizations are characterized by a bimodal sound energy distribution with peaks at 470-970 Hz and 1220-1960 Hz. Six distinct vocalizations are described and putative functions assigned on the basis of 1) context of call and 2) responses to playback experiments. Vocalizations are categorized as consisting of one note (boink, cut), more than one note (series, series growl), or trills (growl, release growl). All vocalizations are

distinguishable on the basis of temporal pattern differences measured on sound spectrograms. The sound pressure levels of each call varied significantly, with growls being the loudest, followed by series growls and series.

Boinks and series vocalizations appear to function as graded advertisement displays. The series growl, a complex call (Wells 1977c), may function as a compound advertisement call, communicating both courtship and aggressive intent. This is the first complex call reported for the family Ranidae. Growl vocalizations appear to communicate aggressive intent, and cuts appear to communicate the locations of interacting males. Release growls appear to function in the same manner of most other anurans: to stimulate the release of an inappropriate clasp.

Comparisons were made among the vocal repertoires of mink frogs and two related species, the green frog, Rana clamitans, and the bullfrog, Rana catesbiana. The vocal behavior of the mink frog is most similar to that of the green frog.

Mink frog populations at all sites investigated showed marked declines in population levels. At two sites in Itasca State Park, Schoolcraft Island and West Twin Lake, mink frog populations declined an order of magnitude over a period of 25 and 15 y, respectively. The decline may have been related to redleg disease, caused by the bacterium

Aeromonas hydrophila. Redleg symptoms were found in 19% of all frogs in 1982, whereas only two dead frogs with redleg symptoms were reported in the late 1960's (Hedeen 1970). The incidence of infected frogs was probably much higher as many leopard frogs (Rana pipiens) carry the disease but are asymptomatic (Hird et al.1981). Juvenile mink frogs showed signs of the disease more frequently than adults. Possibly redleg, combined with some other factor such as severe winters, is an important cause of mink frog mortality. The overall sex ratio was female-skewed. This may have been due to differential predation upon males.

GENERAL INTRODUCTION

The mink frog (Rana septentrionalis), a small- to medium-sized member of the anuran family Ranidae (46 genera, 560 species worldwide; one genus, 21 species in North America), ranges from Labrador to northern New Hampshire and westward to northeastern Minnesota and southeastern Manitoba. The northern limits of its range are unknown (Hedeen 1977).

The mink frog is one of the most nocturnal and aquatic North American ranids (Marshall and Buell 1955; Schmid 1965). The species inhabits areas of slow moving water with dense vegetative cover (Hedeen 1970; Breckenridge 1944), and is found away from water only during rainstorms when individuals sometimes move between bodies of water (Hedeen 1970).

The mink frog oviposits during mid-June to early August (Breckenridge 1944). The tadpole stage lasts 1-2 y, and tadpoles metamorphose from 24 June to 30 August (Wright and Wright 1949; Hedeen 1971) at 29 to 42 mm snout-vent length (SVL) (Hedeen 1977). Females reach maturity at a larger size (54-59 mm) than males (45-50 mm) (Hedeen 1972a).

This species appears sexually dimorphic, both in size (females larger than males) and in tympanum diameter (larger in males, Wright and Wright 1949). Howard (1981) proposed that size dimorphism in bullfrogs (Rana catesbiana) resulted from early maturation of males and high rates of predation on larger (older) males. There are no data addressing the question of age-specific mortality in the mink frog, but males do mature at a smaller size (younger) than females (Hedeen 1972a).

Hedeen (1972a) used a "sex-index" (Martof 1956) based on SVL/tympanum diameter to sex mink frogs in the field. This technique was verified by internal examination of the gonads and found to be accurate for frogs longer than 48 mm (SVL) 98% of the time (Hedeen 1972a). Mink frogs were sexed as: 1) males if the sex-index was less than 10 and the SVL was at least 48 mm, 2) females if the sex-index was at least 10 and the SVL was at least 48 mm, and 3) juveniles if the SVL was less than 48 mm. Tympanum dimorphism occurs in seven of 21 species of North American ranids (Wright and Wright 1949). Tympanum size does not vary seasonally in the mink frog (Hedeen 1972a). Recent work on the acoustic system of the leptodactylid Eleutherodactylus coqui (Narins and Capranica 1976) demonstrated sexual differences in the auditory systems of this sexually dimorphic (tympanum diameter) species. However, no such differences have been found in any North American ranids (Capranica 1976).

At Itasca State Park, mink frogs are first observed on warm days during spring (April-May). On cool days the frogs remain underwater. Reproductive activity occurs from late June to early August (Hedeen 1972a). With the onset of cool weather in fall, adults and juveniles move to overwintering sites in deep water and spend only warm days at the water's surface (Hedeen 1970). This species may not hibernate, as it has been captured mid-winter under ice in minnow traps (J.C. Underhill, pers. comm.).

The objectives of this mink frog study were threefold:

1) to describe the spacing and mating behavior,

2) to describe the acoustic communication system, and

3) to investigate long-term population trends in the Itasca State Park, Minnesota area.

MATING BEHAVIOR OF THE MINK FROG

INTRODUCTION

The mink frog (Rana septentrionalis), a small- to medium-sized member of the anuran family Ranidae (46 genera, 560 species worldwide; one genus, 21 species in North America), ranges from Labrador to northern New Hampshire and westward to northeastern Minnesota and southeastern Manitoba. The northern limits of its range are unknown (Hedeen 1977).

The mink frog is one of the most nocturnal and aquatic North American ranids (Marshall and Buell 1955; Schmid 1965). The mink frog inhabits areas of slow moving water with dense vegetative cover (Breckenridge 1944; Hedeen 1970), and is found away from water only during rainstorms when individuals sometimes move between bodies of water (Hedeen 1970).

The mink frog oviposits during mid-June to early August (Breckenridge 1944). The tadpole stage lasts 1-2 y, and tadpoles metamorphose from 24 June to 30 August (Wright and Wright 1949; Hedeen 1971) at 29 to 42 mm snout-vent length (SVL) (Hedeen 1977). Females reach maturity at a larger size (54-59 mm) than males (45-50 mm) (Hedeen 1972a).

The mink frog is sexually dimorphic, both in size (females larger than males) and in tympanum diameter (larger in males, Wright and Wright 1949). Howard (1981) proposes that size dimorphism in bullfrogs (Rana catesbiana) results from early maturation of males and high rates of predation on larger (older) males. There are no data addressing the question of age-specific mortality in the mink frog, but males do mature at a smaller size (younger) than females (Hedeen 1972a).

Hedeen (1972a) used a "sex-index" (Martof 1956) based on SVL/tympanum diameter to sex mink frogs in the field. This technique was verified by internal examination of the gonads and found to be accurate for frogs longer than 48 mm (SVL) 98% of the time (Hedeen 1972a). Mink frogs were sexed as: 1) males if the sex-index was less than 10 and the SVL was at least 48 mm, 2) females if the sex-index was at least 10 and the SVL was at least 48 mm, and 3) juveniles if the SVL was less than 48 mm.

At Itasca State Park, mink frogs are first observed on warm days during spring (April-May). On cool days the frogs remain underwater. Reproductive activity occurs from late June to early August (Hedeen 1972a). With the onset of cool weather in fall, adults and juveniles move to overwintering sites in deep water and spend only warm days at the water's surface (Hedeen 1970). This species may not hibernate, as

it has been captured mid-winter under the ice in minnow traps (J.C. Underhill, pers. comm.).

Anuran mating behavior has been intensively studied for a number of families (Wells 1977a), including two North American ranids closely related to the mink frog (Moore 1949; Case 1978): the green frog, Rana clamitans (Wells 1977b; 1978), and the bullfrog, Rana catesbiana (Wiewandt 1969; Emlen 1976; Howard 1978a; Ryan 1980). Numerous studies indicate that anuran breeding aggregations can be classified into two categories based on breeding season duration: "prolonged" breeders (long duration) and explosive breeders (short duration; e.g. wood frogs, Rana sylvatica, Howard 1980; Berven 1981) (Wells 1977a). Emlen and Oring (1977) predicted that temporal dispersion of mate availability greatly affected the degree for polygamy. "Prolonged" breeding anurans have been often characterized by male-skewed operational sex ratios (OSR) and territorial defense of calling and/or oviposition sites (Wells 1977a). Therefore, "prolonged" breeders exhibit a greater potential for polygamy than "explosive" breeders; hence "prolonged" breeders may exhibit greater variability in male mating success.

Mating behavior of the mink frog has not been intensively studied. Hedeen (1972a) reported that breeding choruses formed in late May and ended in early August, that

males in breeding habitats shifted locations during the breeding season, and that the OSR was male-skewed due to the short stay of females at the breeding site. Aronson (1943) studied the oviposition behavior of the mink frog in an aquarium.

The primary objectives of this study are to:

1) describe male and female mating behavior,

2) compare mink frog mating behaviors with those of two congeners, the green frog and bullfrog, and

3) compare life history characteristics of the mink frog with those of five sympatric ranids.

MATERIALS AND METHODS

Description of Study Areas

Both study sites (West Arm Bay and enclosure) were bounded by mesic deciduous forest. In addition, West Arm Bay was partially bounded by a floating bog. Both study areas were dominated by sedge (Carex sp.), bulrush (Scirpus sp.), cutgrass (Leersia sp.), bladderwort (Utricularia sp.), water weed (Anacharis sp.), pondweed (Potamogeton sp.), coontail (Ceratophyllum sp.), water milfoil (Myriophyllum sp.), and filamentous algae. Deep water areas consisted of wild rice (Zizania sp.), bulrush (Scirpus sp.), and yellow

water lily (Nuphar sp.). Water depth at both study areas ranged from several cm to 1.5 m at 20 m away from shore.

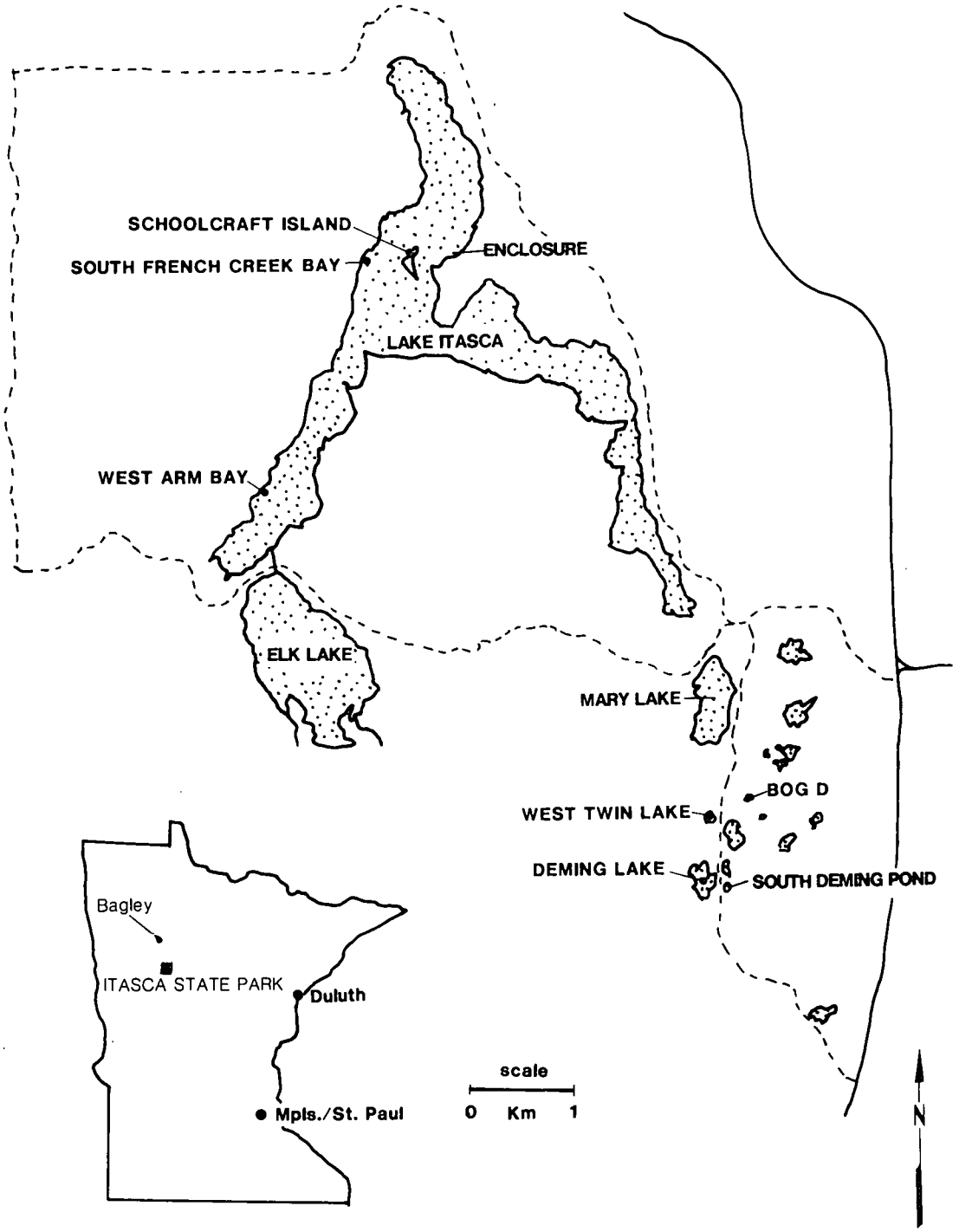
West Arm Bay Population, 1981

Behavioral observations were made on 25 nights from 25 June to 2 August 1981 at West Arm Bay, Lake Itasca (Figure 1). Observations were made between 22:30 h and 04:00 h at a small, naturally-occurring chorus of three to five calling males per evening. The study site was approximately 1620 m^2 in size.

Frogs were found with the aid of headlamps and hand-held lanterns, and were caught by hand from a canoe. Frogs were individually marked via toe-clipping (Martof 1956) and waist tags (Figure 2). Tags (made of plastic flagging) with large (1.5 cm in length) numerals were tied around the waists of frogs with cotton string to facilitate individual recognition at a distance. Frogs were measured (tympanum diameter to the nearest 0.5 mm, snout-vent length [SVL] to the nearest 1.0 mm) and weighed (to the nearest 0.25 g).

Frog locations were mapped each night to the nearest meter using a coordinate grid system of string suspended approximately 0.5 m above the water, with orange flagging at 1 m intervals. Focal animal sampling (Altmann 1974) was used whenever uncommon behaviors (fights, amplexes) were

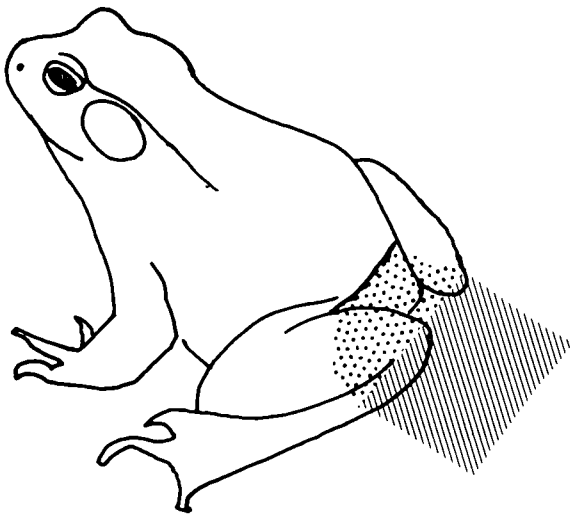
Figure 1: Sites of behavioral studies on Lake Itasca in northwestern Minnesota; West Arm Bay was the location of the 1981 study, enclosure site was location of 1982 study


SCHOOLCRAFT ISLAND
SOUTH FRENCH CREEK BAY
ENCLOSURE
LAKE ITASCA
WEST ARM BAY
ELK LAKE
MARY LAKE
BOG D
WEST TWIN LAKE
DEMING LAKE
SOUTH DEMING POND
Bagley
ITASCA STATE PARK
Duluth
Mpls./St. Paul
scale
0 Km 1
N

observed. Observations were only possible using headlamps and hand-lanterns. Since intense light altered calling frequency, indirect (diffuse) light was utilized to monitor activities.

Various SAS computer programs were used in data analyses (SAS Institute 1982a, 1982b), and several nonparametric tests were employed (Siegel 1956). A critical level of statistical significance of $P<0.05$ was used to reject null hypotheses.

Figure 2: Diagram of waist tags used for individual identification of mink frogs



1982 TAG

1981 TAG

Enclosure Population, 1982

In 1982, a 19 X 14 m enclosure was constructed of 91.4 cm wide hardware cloth (1.3 cm mesh) along the east shore of Lake Itasca (Figure 1). The wire was attached to wooden stakes driven into the lake bottom and anchored to cement blocks. An observation tower was constructed from steel scaffolding (2.5 m above the water) in order to facilitate behavioral observations.

The enclosure was stocked with 32 mink frogs (10 males, 22 females) from South Deming Pond (the total population of the pond; Figure 1). The resulting density approximated that found on Schoolcraft Island (Figure 1) in the late 1950's (MacDonald and Engebretson 1959). Midway through the breeding season, 10 calling males were added to the enclosure in an attempt to increase the rate of interactions. All individuals were marked as in 1981, but waist tags were shortened in order to avoid interference with oviposition (Figure 2).

Observations were made on 16 nights from 29 June to 22 July 1982, mainly between 23:00 h and 04:00 h. A grid system similar to that in 1981 was constructed, and focal animal sampling was used. Egg masses were intensively searched for. Data from several unpublished class reports

were included for comparative purposes (Lemmerman and White 1958; MacDonald and Engebretson 1959; McKee 1962; McKenzie 1962; Wunderle and Wenstrom 1970; Peacock and Drake 1971; Baird et al. 1972; Lewis 1972; Priemer et al. 1973; Caponi 1976; Carroll 1976; Kelling 1976).

Commentary on 1981 Methods

The population of West Arm Bay (1981) had 35 individuals (14 males, 19 females, 3 juveniles) in an area of 1620 m^2. Few fights (N=4), no amplexes, and one partial egg mass were observed. Waist tags used (Figure 2) were too long and interfered with oviposition.

Commentary on 1982 Methods

More fights, amplexes, and oviposition were observed in 1982 than in 1981. However, the enclosure constructed in 1982 was only partially successful. Many individuals escaped by climbing over or diving under the fence. Males appeared attracted by distant choruses. Most individuals that escaped were not seen again, but a few established territories outside the enclosure. Waist tags used in 1982 were considered to be superior to those used the previous year as evidenced by the successful oviposition observed and the decreased rate of tag loss.

Definitions

For the purposes of this paper, a territory is defined as any defended area. A chorus is any group (> 1) of calling frogs. Calling sites are specific locations of calling males, more than one of which may be found in a territory. Jump attacks describe the behavior of one male jumping on the back of another frog. Head-butting describes snout-snout contact of fighting males. Wrestling involves throat-throat and venter-venter contact of males maintained by interlocked forelimbs. Counter-calling is the alternation, usually without overlap, of vocalizations between two or more males (Wells 1977b).

RESULTS

Male Behavior and Territoriality

Male mink frogs were rarely observed in deep water during the day, but at sunset (22:00 h to 23:00 h) they moved from shallow diurnal sites into deeper water (approximately 1 m. depth) and established territories. Mink frogs at Lake Itasca chorused from 24 June to 17 August in 1981, and from 22 June to 15 August in 1982.

Only 29% (4/14) of the males at West Arm Bay defended territories (via vocalizations or overt aggression). This resulted in a highly variable duration of stay of males at the chorus ($\bar{x}$= 8.3 days, SD=6.78 days, N=10). Males that

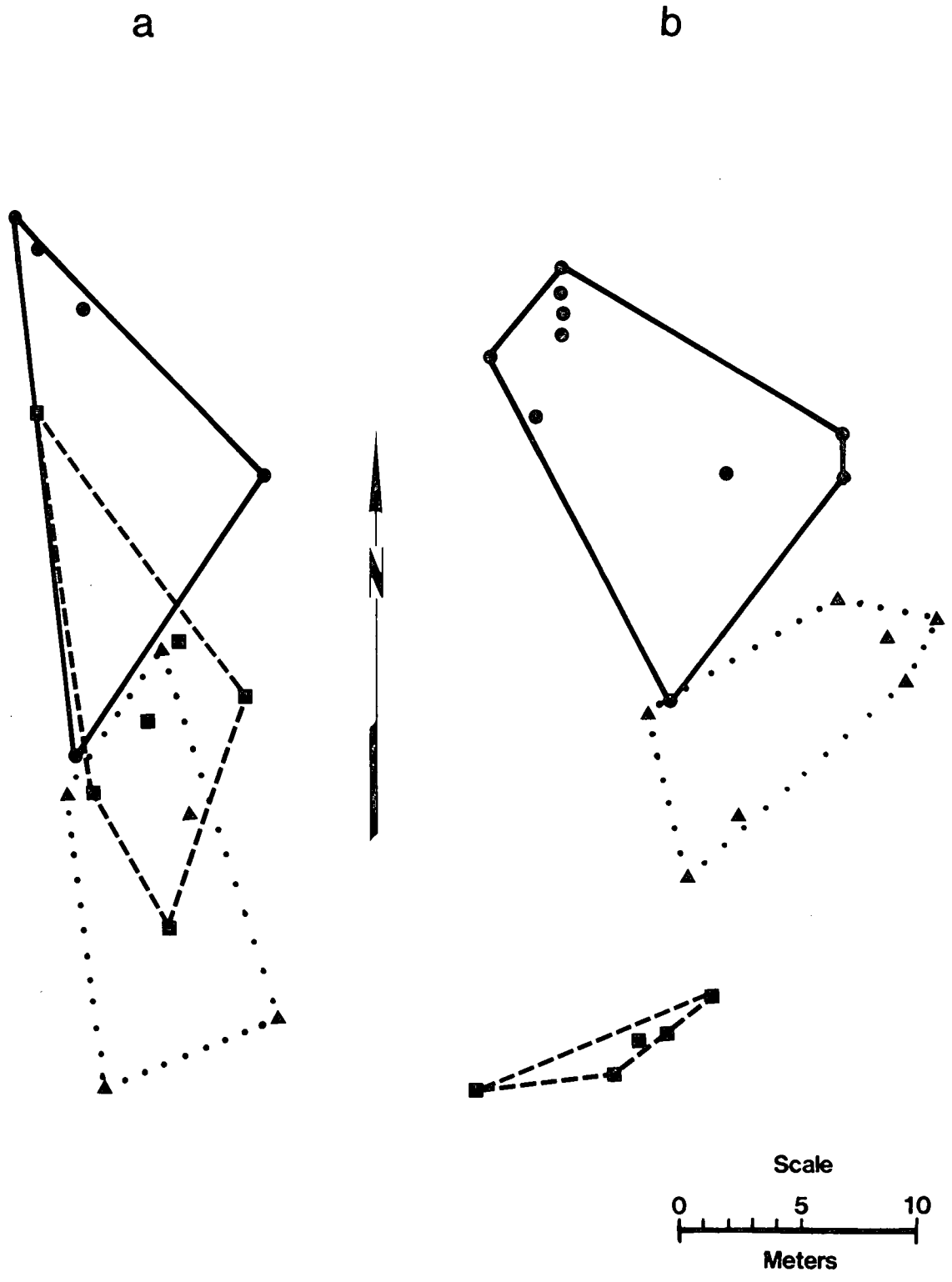
spent more than the mean number of days at the chorus defended one territory and a mean of 9.75 (SD=5.62, N=4) calling sites within that territory throughout the breeding season. Territorial boundaries changed in location throughout the breeding season (Figure 3).

Calling males were nonrandomly distributed (West Arm Bay) ($P<0.05$, chi^2 test for goodness of fit to Poisson distribution). The nearest neighbor distances (NND's) were significantly greater for calling males than non-calling males (Tables 1 and 2). Non-calling males were never tolerated closer than 1 m to calling males, nor were they ever observed to intercept females. Based on the mean NND of 9.3 m (SD=7.0 m, N=62) for calling males, a circular territorial area of 272 m^2 was calculated (area=pi[r^2]). Because of the high density of enclosed frogs in 1982, the mean NND for the enclosure site animals (2.1 m) was lower than those at West Arm Bay.

Vocal interactions (59% of total number of agonistic encounters) took the form of counter-calling: two or three males alternated their vocalizations without temporal overlap. Counter-calling occurred when territorial males were spaced several ($\bar{x}$= 9.3 m) meters apart.

Overt aggression was observed between males whenever they moved within 1 m of each other. Territorial males did displace other terriorial males:

Figure 3: Diagram of individual male locations and territory locations of three males at West Arm Bay, 1981; a=1 July to 10 July, b=11 July to 3 August, solid line=male #4, dashed line=male #7, dotted line=male #10


a
b
N
Scale
0
5
10
Meters

Male #4 occupied an exclusive area from the initiation of observations (1 July 1981) until 6 July. On 6 July, another male (#10) moved into male #4's territory. Males #4 and #10 counter-called and fought on four nights. On 10 July, male #4 lost a very intense fight with male #10. For the duration of the breeding season, male #10 occupied the territory previously occupied by #4, and #4 was not found calling, but remained in the vicinity of the chorus (Figure 3).

Fights consisted of jump attacks, head butting, wrestling, clasping, and chases, interspersed with high intensity vocalizations (Chapter II). Although I observed no wrestling bouts between mink frogs, they were reported by others (Priemer et al. 1973; Carroll 1976; Kelling 1976; Lewis 1972).

Figure 4 illustrates the typical sequence of events of agonistic encounters between males. Males that remain in the vicinity of the fight and call are designated winners. Losing males invariably adopt low postures and do not vocalize. Careful observation of the relative orientation of interacting males did not reveal use of reciprocal displays of the yellow throat region.

TABLE 1

Summary of Wilcoxon 2-Sample tests for categories of nearest-neighbor distances for the West Arm Bay population (1981); nearest-neighbor distances for the enclosure (1982) are not included in this analysis

	Nearest-neighbor distance		
	Categories		
Categories	Calling males	Non-calling Males	Females
All males	P=0.050 S=7753.00 z=1.96	NS	P=0.008 S=17039.00 z=2.64
Calling males	---	NS	P<0.01 S=7362.50 z=3.84
Non-calling males	---	---	P=0.01 S=10169.50 z=2.58

TABLE 2

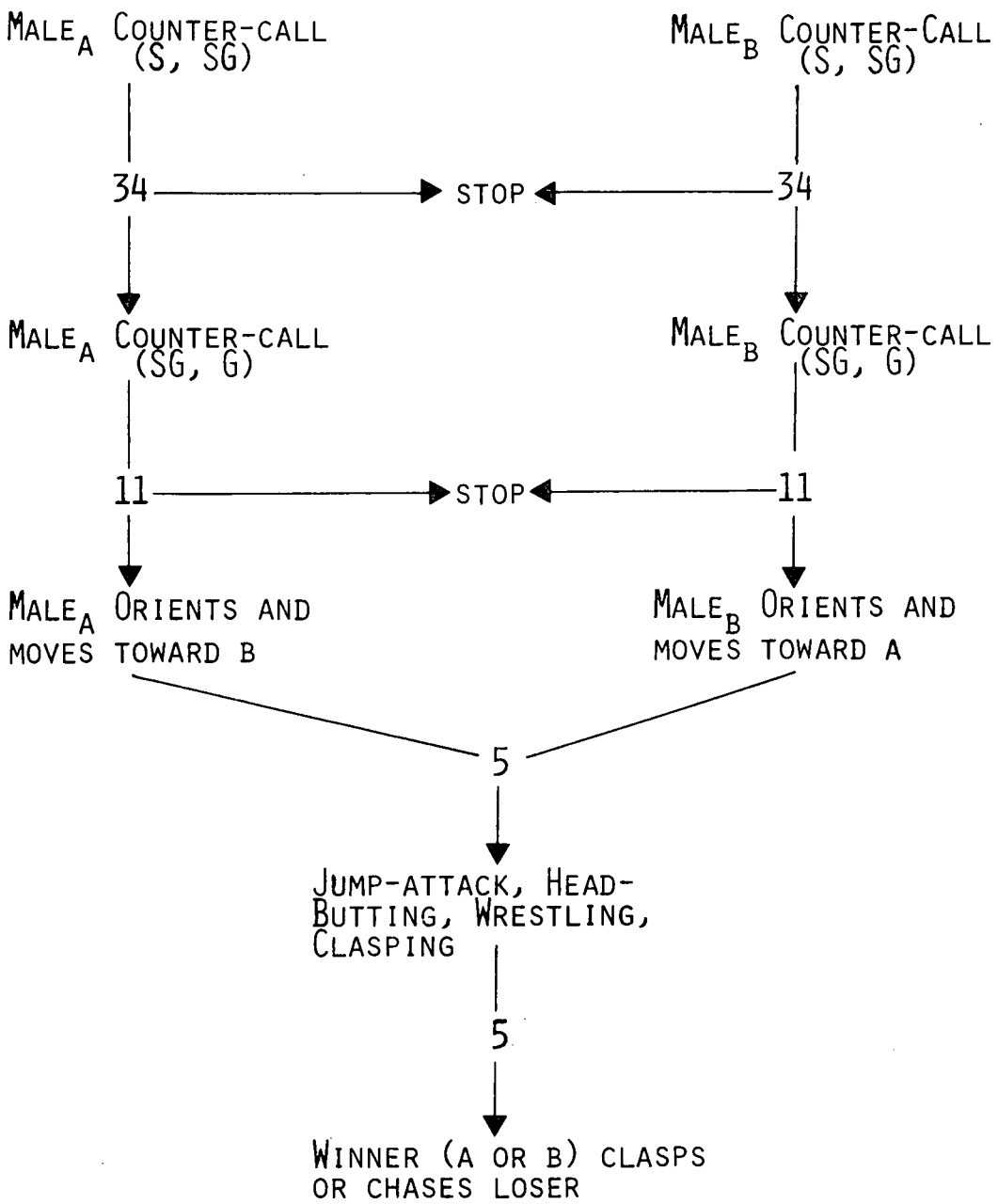
Mean nearest-neighbor distances for calling males, non-calling males, females (West Arm Bay, 1981), and both sexes for 1982 (enclosure)

Category	Mean NND (m)
Calling males	9.3
Non-calling males	8.6
Females	5.6
Enclosure (1982)	2.1

The outcomes of five fights were observed (two in 1981, three in 1982). Although snout-vent length (SVL) was not significantly associated with winners of fights ($P>0.05$, Mann-Whitney U-test), weight was ($p=0.031$, $N=5$, Sign Test). Male weight correlated significantly with SVL ($P<0.001$, Pearson's $r=.762$, $N=44$), indicating that the lack of association between SVL and winners of fights may have resulted from too few observed fights. Other male characteristics did not correlate with winning, including the number of nights spent calling and the number of days spent at calling sites ($P>0.05$, Mann-Whitney U-test).

The frequency of male amplexus was highly variable (mean number of mates=1.3, $s^2=17.11$, SD=4.24, N=20). Males that amplexed at least once amplexed a mean of 2.0

Figure 4: Typical sequence of events in male agonistic encounters; S=series vocalization, SG=series growl vocalization, G=growl vocalization (chapter II)


MALE A COUNTER-CALL (S, SG)
MALE B COUNTER-CALL (S, SG)
34
STOP
34
MALE A COUNTER-CALL (SG, G)
MALE B COUNTER-CALL (SG, G)
11
STOP
11
MALE A ORIENTS AND MOVES TOWARD B
MALE B ORIENTS AND MOVES TOWARD A
5
JUMP-ATTACK, HEAD-BUTTING, WRESTLING, CLASPING
5
WINNER (A OR B) CLASPS OR CHASES LOSER

times (s^2=0.8, SD=1.0, N=5). Male characteristics that might have influenced the amplexus frequency/male including 1) the number of nights calling, 2) size (SVL and weight), 3) site tenacity (number of nights spent at each calling site), and 4) vocalization characteristics were investigated. None were significantly related to the frequency of male amplexus (P>0.05, Mann-Whitney U-test).

Female Behavior, Amplexus, and Oviposition

Female mink frogs were neither aggressive nor territorial. They were behaviorally cryptic, hiding in dense vegetative cover at all times of the day. Females did not spend a significantly different number of days at the breeding chorus than males, but the operational sex-ratio (OSR: ratio of sexually active males to fertilizable females at any given time, Emlen and Oring 1977) was strongly male-skewed due to the short duration of female breeding readiness (McKee 1962). The OSR varied from 5:0 to 3:1 over the breeding season. Nearest-neighbor distances of females ($\bar{x}$= 5.6 m) were significantly smaller than those of males (Tables 1 and 2), and females tended to be more clumped than males.

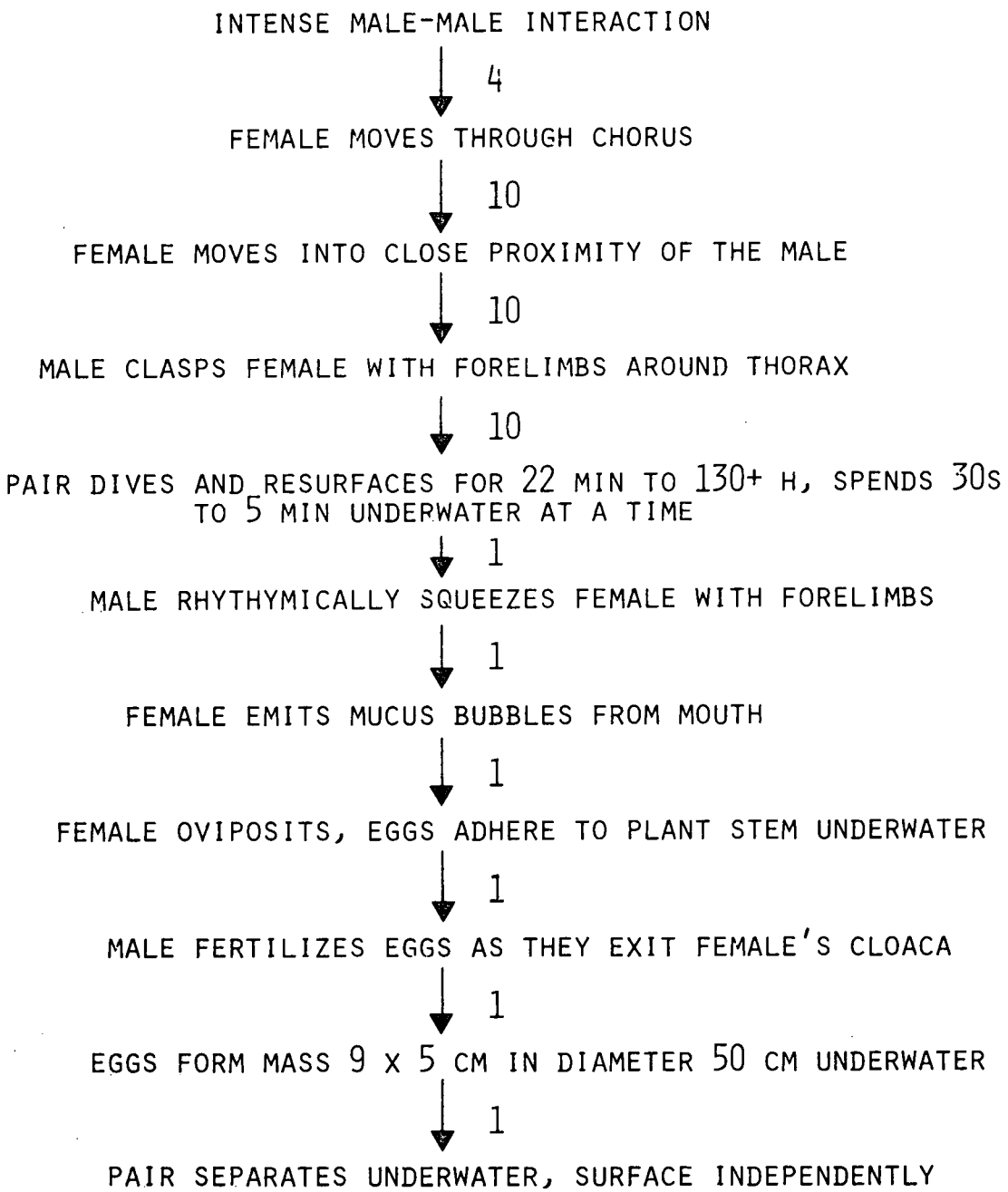
Females were observed moving through the West Arm Bay breeding chorus on four occasions. Ten amplexes were

Figure 5: Typical sequence of events of mink frog amplexus

observed from 2 July to 13 July 1982. Amplexes were initiated between 24:30 h and 04:12 h and lasted from 22 min to longer than 130 h. The 22 min amplexus resulted in the only successful oviposition observed. This oviposition occurred in the vicinity of an intense three-way male agonistic interaction, and it was not known whether the amplexed male was the winner of the fight. A partial egg mass was discovered attached to the free waist tag of a territorial male in 1981. The tag was found within the male's territory. Apparently, females oviposited within the male's territory.

With regard to size, amplexed females were significantly longer than amplexed males ($P=0.031$, $T_S=0$, $N=5$, Wilcoxon Signed-Ranks test). Hence, the larger female appeared to control the movement of the amplexed pair. Figure 5 shows a typical sequence of events of amplexus.

Figure 5: Typical sequence of events of mink frog amplexus


INTENSE MALE-MALE INTERACTION
4
FEMALE MOVES THROUGH CHORUS
10
FEMALE MOVES INTO CLOSE PROXIMITY OF THE MALE
10
MALE CLASPS FEMALE WITH FORELIMBS AROUND THORAX
10
PAIR DIVES AND RESURFACES FOR 22 MIN TO 130+ H, SPENDS 30S TO 5 MIN UNDERWATER AT A TIME
1
MALE RHYTHYMICALLY SQUEEZES FEMALE WITH FORELIMBS
1
FEMALE EMITS MUCUS BUBBLES FROM MOUTH
1
FEMALE OVIPOSITS, EGGS ADHERE TO PLANT STEM UNDERWATER
1
MALE FERTILIZES EGGS AS THEY EXIT FEMALE'S CLOACA
1
EGGS FORM MASS 9 X 5 CM IN DIAMETER 50 CM UNDERWATER
1
PAIR SEPARATES UNDERWATER, SURFACE INDEPENDENTLY

DISCUSSION

Mink Frog Mating Behavior

Explosive vs Prolonged Breeders

Anuran mating patterns have been classified as "prolonged" and "explosive" (Wells 1977a). Populations of "prolonged" breeders generally reproduce in relatively permanent bodies of water and have a breeding season greater than one month. "Explosive" breeders, on the other hand, reproduce in ephemeral habitats for periods less than a month (Wells 1977a).

Male mink frogs chorus from mid-June to early August (Hedeen 1972a; present study), and female mink frogs ovulate from 15 June to 30 July (McKee 1962). Thus, the mink frog is categorized as a "prolonged" breeder. So too are its two close relatives, the green frog and bullfrog (Moore 1949; Case 1978) (Wells 1977a).

Territoriality

Male mink frogs competed intensively for specific territory sites. Fights between territorial males occurred, and the loss of a territory by a resident male (male #4) was observed once. The victorious male (male #10) subsequently occupied this site for the duration of the breeding season.

This territory turnover, coupled with defense of stationary sites indicate strong attachment of males to specific sites.

Female oviposition within the amplexing male's territory supports the notion of male defense of ovipostion sites. Male green frogs and bullfrogs were less site tenacious, but females similarly oviposited within the amplexing male's territory (Emlen 1976; Wells 1977b; Howard 1978b).

Green frog and bullfrog territory changes resulted from: 1) aggressive encounters and 2) deterioration of the thermal/vegetative environment of oviposition sites (Wells 1977b; Howard 1978a). Since the only observed mink frog territory turnover resulted from an aggressive encounter, deterioration of mink frog territory quality did not appear to occur.

The apparent lack of deterioration of mink frog territory quality may be explained by differences in chorus location of the three species. Green frogs and bullfrogs chorused on small, shallow ponds (Wells 1977b; Howard 1978a), whereas the West Arm Bay mink frog chorus was located on a bay of a large lake. Such large bodies of water probably do not undergo as drastic changes in habitat quality as were experienced by green frogs and bullfrogs in the studies by Wells (1977b) and Howard (1978a).

Duration of stay of non-territorial males at the breeding chorus is highly variable (Priemer et al. 1973; Kelling 1976; present study). This phenomenon may be related to the availability of suitable territories. In green frogs (Wells 1977b) and bullfrogs (Howard 1978a) oviposition site (and therefore territory) quality varies spatially and seasonally. Female bullfrogs select oviposition sites that minimize developmental abnormalities and maximize embryo survivorship (Howard 1978a). If these same criteria are utilized by mink frog females for oviposition site selection, and the number of suitable sites are rare, then the potential for monopolization of these sites by a small number of males exists. Males that are not successful in acquiring female-preferred oviposition sites may be forced to 1) utilize male mating strategies other than territoriality (not observed in the mink frog, but see Wells 1977b; Howard 1978a) or 2) relocate at another chorus and attempt to establish a new territory. Number 2) above may explain the variable duration of stay at the chorus of non-territorial mink frogs.

Non-Territorial Males

A significant number of male mink frogs did not defend breeding territories. Just 28% of the males at West Arm Bay in 1981 were territorial; and only half (50%) of the males in a comparable study were territorial (Carroll 1976).

The proportion of territorial males in a population may be associated with such factors as availability/defendability of required resources, population density, and population sex-age structure. At least one male mink frog switched from being territorial to non-territorial after being defeated in a fight. Other non-territorial males initially may have failed to establish territories due to relatively low competitive ability. Non-territorial males were not observed amplexing with females.

Non-territorial green frog males utilized a "satellite" strategy. Such males moved close to territorial males, adopted low postures, and took over vacated territories (Wells 1977b). However, they were not observed amplexing with females. Bullfrog males utilized three mating strategies: 1) territoriality, 2) male parasitism, and 3) opportunism (Howard 1978a). Male bullfrog "parasitic" behavior was the same as the green frog "satellite" behavior (Wells 1977b). "Opportunistic" males called from specific sites, but did not defend them from rival males. Territorial bullfrog males were larger than males utilizing other mating strategies. Male mating success was highest for territorial males, lowest for "parasitic" males, and intermediate for "opportunistic" males (Howard 1978a).

Spacing Patterns

Nearest-neighbor distances of calling (territorial) and non-calling (non-territorial) males appeared to be related to differences in cues used in the detection of neighbors. Calling males used auditory cues as the primary means of maintenance of individual spacing patterns. Non-calling males, with their associated smaller NND's, may have used auditory cues to locate territorial males, but were restricted to visual cues for non-calling mink frog detection, hence their significantly smaller NND's. Females did not show any signs of neighbor avoidance. This lack of spatial antagonism may have resulted in the very small NND's of females.

Nearest-neighbor distances appeared to vary with population density. In 1981, at low population levels (Chapter III), the mean NND of calling males was 9.3 m, indicating a circular territory area of 272 m^2. Nearest-neighbor distances in 1976 (at higher population levels) were 3-4 m (Carroll 1976) and a mean of 6.5 m (N=33, Caponi 1976), hence territory size ranged from 28-132 m^2. Mink frog territory size at low population densities (1981) was larger than both green frog (3-113 m^2, Wells 1977b) and bullfrog (28-113 m^2, Wells 1977a) territory sizes. Given the plasticity of mink frog spacing patterns, direct comparisons with green frog and bullfrog spacing patterns is probably not meaningful.

Fighting

Mink frog fights were less intense (no wrestling bouts observed) and shorter when population levels were low (1981-2) than when they were high (1960's-70's). Low numbers of females present at the chorus may have resulted in lower variance of male mating success. With low variance of male mating success, the cost/benefit ratio of intense fighting may have increased, leading to fewer, less intense fights. Intense mink frog fights appeared to incur a great cost to the loser as evidenced by the outcome of the extended interaction between male #4 and male #10. The cost of losing for male #4 was the loss of the ability/motivation for territorial defense and its probable associated lack of reproductive success.

Mink frogs defended territories with a combination of vocal and physical interactions, a characteristic shared with the green frog and bullfrog (Emlen 1968; Wiewandt 1969; Emlen 1976; Wells 1977b; Howard 1978a; Wells 1978; Ryan 1980). Vocal communication was utilized exclusively at moderate distances. Overt aggression (mink frog, green frog, bullfrog) and visual displays (green frog, bullfrog) were utilized for short distance interactions.

Mink frog agonistic encounters were similar to those of the green frog and bullfrog with the following exceptions:

1) Mink frog wrestling bout duration (3-4 s, Priemer et al. 1973) was similar to that of green frogs (Wells 1978), but shorter than that of bullfrogs (Emlen 1976).

2) Unlike mink frogs (Wunderle and Wenstrom 1970; Priemer at al. 1973; Caponi 1976; present study), green frogs (Wells 1978) and bullfrogs (Emlen 1976) used reciprocal displays of yellow throat regions.

3) Unlike mink frogs, green frogs (Wells 1978) and bullfrogs (Wiewandt 1969) used loud splashing and jumping displays to advertise territory locations.

Weight (and therefore length) was a good predictor of fighting success for male mink frogs. In green frogs and bullfrogs, larger males also won more fights than smaller males (Wells 1977b; Howard 1978a).

Female Behavior

Female mink frogs were neither aggressive nor territorial, but were observed on four occasions moving unobtrusively through the breedig chorus, eliciting no observable male reponse. Similar behaviors have been reported for green frogs (Wells 1977b) and bullfrogs (Emlen

1976; Howard 1978a), with the exception of female bullfrog aggressive behavior (Capranica 1968).

Female mink frogs remained at the West Arm Bay breeding chorus as long as males in 1981. However, when mink frog population levels were higher in the 1960's, females did not remain at the chorus for more than a couple of days (Hedeen 1972a). It has been demonstrated that social stimuli (e.g. vocalizations) elicit hormone production in anuran gonads (Brzoska and Obert 1980). Female mink frogs may have remained longer at the smaller (fewer calls/unit time) chorus before coming into reproductive readiness than at the larger (1960's) choruses. Bullfrog females did not remain at breeding choruses for longer than a day or two (Emlen 1976; Howard 1978a).

Mink Frog Mating System

The mink frog OSR in 1981 at West Arm Bay was male-skewed due to the short duration of female breeding readiness (McKee 1962). Even though females remained at the chorus as long as males, only a few females were ready to mate on a given evening. The OSR's of both green frogs (Wells 1977b) and bullfrogs (Emlen 1976; Howard 1978a) also were male-skewed. Therefore, variance in male mating success and the degree of polygamy in all three of these species was expected to be relatively high (Emlen and Oring 1977).

Male mating success (or frequency of amplexus) was highly variable in mink frogs ($\bar{x}$= 1.3 mates, SD=17.11 mates). Variations in mink frog territory quality were not investigated, so the relationship between territory quality and male mating success awaits further research. No male mink frog characteristics investigated (number of nights called, weight, SVL, site tenacity, vocalization characteristics) correlated with the frequency of amplexus. Male mating success in green frogs was also variable ($\bar{x}$= 0.80, SD=1.00 mates, N=46, Wells 1977b) and was related to territory quality (not male size). Male bullfrog mating success (0-4 mates, Howard 1978a) was associated with large body size, which in turn was associated with high territory quality. The factors determining mink frog male mating success appear to be more closely tied to those of the green frog (territory quality disassociated from male quality) than the bullfrog.

The mating system of the mink frog is tentatively classified as resource defense polygyny (Emlen and Oring 1977) for the following reasons: 1) female mink frogs appear to oviposit within the amplexing male's territory, 2) male mink frog mating success (measured by frequency of amplexus) is variable, and 3) male mating success appears to be related to territory quality (no male characteristics were associated with the frequency of amplexus).

Natural History as Related to Other North American Ranids

The mink frog is sympatric with the following ranids over parts of its range: green frog, bullfrog, northern leopard frog (Rana pipiens), pickerel frog (Rana palustris), and wood frog (Rana sylvatica). Of the above species (except the pickerel frog; no studies comparing its water economy with the mink frog are available), the mink frog is the most aquatic adapted as determined by comparative water economics (Schmid 1965) and habitat preferences (Marshall and Buell 1955; Hedeen 1970). The mink frog also is as nocturnal, or more so, than any other North American ranid. Mink frog chorus activity does not start until 22:30-23:00 h and few interactions occur before 24:00 h. Peak calling and interactions (fighting, mating) occur between 01:00 h and 04:00 h, ending abruptly at dawn (Chapter III). Other species chorus late at night (e.g. bullfrog, Howard 1978a), but no other North American ranid shows peak chorus activity synchronized with the darkest hours of the night.

Mink frogs are characterized by a foul-smelling musky odor, especially noticeable in large, gravid females. The two major potential fish predators of the mink frog in the Lake Itasca region are the primarily diurnal northern pike (Esox lucius) and the largely crepuscular largemouth bass (Micropterus salmoides). However, mink frogs appear to be unpalatable to these predators based on the frequent

ingestion by these fish of other frogs (e.g. northern leopard frogs) and their lack of feeding responses to mink frogs (L.W. Oring, pers. comm.).

During the day, mink frogs occupy the shallow littoral zone near shore, perhaps in response to heavy duirnal predation pressures from the great blue heron (Ardea herodias) (Hedeen 1971). Mink frogs are easily located during the day in deep water, but are extremely cryptic and difficult to locate in dense vegetation close to shore.

At night, mink frog males defend deep water (1-2 m) sites that appear to be required by females for oviposition. Mink frog egg masses are submerged and globular, and have been found attached to plant stems 20-150 cm underwater (Breckenridge 1944; Wright and Wright 1949; Hedeen 1970; present study). Deep water appears to be a prerequisite for mink frog oviposition. The green frog (Wells 1977b), northern leopard frog, pickerel frog, and wood frog (Wright and Wright 1949) oviposit in shallow water near shore. Bullfrog egg masses, like mink frog egg masses, have been found in relatively deep water (Wright and Wright 1949).

The two ranids that breed farther north than the mink frog (northern leopard frog, wood frog) are early season, "explosive" breeders (Merrell 1977; Howard 1980; Berven 1981) that metamorphose before the onset of winter. The mink frog is the most northerly distributed ranid that

overwinters at the tadpole stage. The delay of the onset of breeding activities until mid summer when lake water temperatures increase to a suitable level may preclude the possibility of metamorphosing before winter.

CONCLUSIONS

This report descibes mink frog mating behavior for the first time. Mink frogs are "prolonged" breeders and their mating system is tentatively described as resource defense polygyny. The mink frog mating behavioral repertoire is more similar to that of the green frog than the bullfrog. This may be due to differences in size (bullfrogs are larger at maturity than both green frogs and mink frogs) and distribution (the range of the green frog more closely matches that of the mink frog). Mink frog occupation of extremely aquatic habitats and northern latitudes result in a unique combination of life history characteristics including: noxious odor/taste, deep water oviposition, nocturnal behavior, late breeding season, and 1-2 y duration of the tadpole stage. Study of larger mink frog populations, especially where sympatric with green frogs, is needed to substantiate these findings and to establish the factors determining mink frog male mating success.

SUMMARY

Mink frogs of both sexes inhabit the shallow littoral zone during the day. At sunset, males move into deep water territories where oviposition occurs. (Wright and Wright 1949; Hedeen 1970).

Males at West Arm Bay, Lake Itasca, chorused from 24 June to 17 August 1981 and from 22 June to 15 August 1982. Because of this long chorus duration and the long period of female ovulation (15 June to 30 July, McKee 1962), mink frogs are classified as "prolonged" as opposed to "explosive" breeders (Wells 1977a).

Even though males did not spend more days at the breeding chorus than females, the operational sex ratio (OSR) was skewed toward males based on the low number of reproductively ready females on any given day (females are fertile only a short time, McKee 1962).

Only 28% (4/14) of all males were territorial in 1981. Those males that were territorial defended one territory for the duration of the season, utilizing a mean of 9.75 calling sites within that territory. Males were site tenacious, and some sites appeared to be preferred over others as evidenced by the aggressive displacement of the resident and subsequent occupation of the site by the victorious male.

Both sexes were non-randomly distributed throughout West Arm Bay (1981). Calling males were spaced significantly farther apart than non-calling males, and non-calling males were spaced farther apart than females. Based on a mean nearest-neighbor distance of 9.3 m for calling males, the mean circular mink frog territory size was approximately 272 m^2.

Over half (59%) of all aggessive encounters were vocal, in the form of counter-calling. The rest involved overt physical aggression, consisting of jump attacks, head-butting, wrestling, clasping, and chases. Heavy males won significantly more fights than light males, and losing males adopted low, unobtrusive postures in the water. Male amplexus success was highly variable ($\bar{x}$= 1.3 females, SD=4.24), but no relationships between male characteristics and amplexus success were isolated.

Female mink frogs were neither aggressive nor territorial. They were behaviorally cryptic at all times of the day and on four occasions were observed moving unobtrusively through the breeding chorus. The events of a mink frog amplexus were described in the wild for the first time. The locations of one complete and one partial egg mass indicated that females oviposited within the amplexing male's territory. A similar result was found for the green frog and bullfrog. The mating system was described as a

resource defense polygyny based on Emlen and Oring's (1977) classification.

Mating behavior of the mink frog was similar to that of the green frog and bullfrog, with several exceptions:

1) Mink frog territory size at low population densities was larger than green frog and bullfrog territory size, but was comparable in size at higher mink frog densities.

2) Mink frog wrestling bout duration was comparable to that of the green frog, but shorter than that of the bullfrog.

3) Mink frogs did not appear to use vocal pouch visual displays during male-male aggressive interactions, in contrast to the green frog and bullfrog.

4) Mink frogs did not utilize jumping and loud splashing displays to advertise territory location, again contrasting with both the green frog and bullfrog.

The unique combination of mink frog life history characteristics (noxious odor, deep water oviposition, nocturnal behavior, late breeding season, 1-2 y duration of the tadpole stage) may have resulted from occupation of extremely aquatic habitats and norhtern latitudes.

MINK FROG VOCAL REPERTOIRE

INTRODUCTION

The mink frog (Rana septentrionalis), a small- to medium-sized member of the anuran family Ranidae (46 genera, 560 species worldwide; one genus, 21 species in North America), ranges from Labrador to northern New Hampshire and westward to northeastern Minnesota and southeastern Manitoba. The northern limits of its range are unknown (Hedeen 1977).

The mink frog is one of the most nocturnal and aquatic North America ranids (Marshall and Buell 1955; Schmid 1965). This species inhabits areas of slow moving water with dense vegetative cover (Breckenridge 1944; Hedeen 1970), and is found away from water only during rainstorms when individuals sometimes move between bodies of water (Hedeen 1970).

The mink frog oviposits during mid-June to early August (Breckenridge 1944). The tadpole stage lasts 1-2 y, and tadpoles metamorphose from 24 June to 30 August (Wright and Wright 1949; Hedeen 1971) at 29 to 42 mm snout-vent length (SVL) (Hedeen 1977). Females reach maturity at a larger size (54-59 mm) than males (45-50 mm) (Hedeen 1972a).

Hedeen (1972a) used a "sex-index" (Martof 1956) based on SVL/tympanum diameter to sex mink frogs in the field. This technique was verified by internal examination of the gonads and found to be accurate for frogs longer than 48 mm (SVL) 98% of the time (Hedeen 1972a). Mink frogs were sexed as: 1) males if the sex-index was less than 10 and the SVL was at least 48 mm, 2) females if the sex-index was at least 10 and the SVL was at least 48 mm, and 3) juveniles if the SVL was less than 48 mm.

Tympanum dimorphism occurs in seven of 21 species of North American ranids (Wright and Wright 1949). Tympanum size does not vary seasonally in the mink frog (Hedeen 1972a). Recent work on the acoustic system of the leptodactylid Eleutherodactylus coqui (Narins and Capranica 1976) demonstrated sexual differences in the auditory systems of this sexually dimorphic (tympanum diameter) species. However, no such differences have been found in any North American ranids (Capranica 1976).

Many species of anurans have vocal repertoires consisting of several different vocalizations (Bogert 1960; Blair 1968; Wells 1977c). Vocal repertoires consisting of up to four calls are common (Salthe and Mecham 1974), and some anurans have more. For example, the green frog (Rana clamitans) is considered to have a vocabulary of five calls (Wells 1978), the bullfrog (Rana catesbiana) six (Capranica

1968; Wiewandt 1969), and the leopard frog (Rana pipiens) eight (Schmidt 1968).

Descriptions in the literature of the mink frog vocal repertoire are inadequate. Wright and Wright (1949) described mink frog calls as resembling "closely the sound produced by striking a long nail on the head with a hammer driving it into heavy timber", a "cut-cut, with sometimes a 'burred' gh-r-r-r", and "rapid squeaking croak." A single audio spectrogram of a mink frog call is found in Hedeen's (1977) SSAR Catalogue account of the mink frog. Several unpublished undergraduate reports at the Lake Itasca Forestry and Biological Station in Itasca State Park, Minnesota describe mink frog vocalizations (Wunderle and Wenstrom 1970; Peacock and Drake 1971; Baird et al. 1972; Priemer et al. 1973; Carroll 1976; Kelling 1976).

The primary objectives of this report are to:

1) describe mink frog vocalizations structurally and functionally,

2) compare the mink frog vocal repertoire with those of the green frog and bullfrog, and

3) describe the first compound advertisement call reported in the family Ranidae.

MATERIALS AND METHODS

In June-August 1981-1982, mink frog vocalizations were recorded from a canoe using a Uher 4000 report-L tape recorder and a Uher 514 dynamic microphone. Tape speed was set at 4.8 cm/s and vocalizations were recorded onto 1 mm thick magnetic tape. Individual subjects were marked, weighed, and measured (snout-vent length and tympanum diameter). The social context of most recorded vocalizations were noted and were described elsewhere (chapter II).

Sound spectrograms were made using a Kay Electronics 7029A sound spectrum analyzer, with amplitude display (loudness vs time), scale magnification, and sectioner (frequency vs loudness) options. All temporal pattern measurements were made (to the nearest 0.003 s) from sound spectrograms produced at wide band settings. Narrow band sound spectrograms were used for preliminary descriptions of call spectrographic qualities. The sectioner was used to measure dominant (loudest) frequencies of each call to the nearest 91 Hz, and amplitude displays measured to the nearest 1.3 dB were used to determine maximum changes in sound-pressure-levels (SPL, dB) throughout each vocalization containing trills.

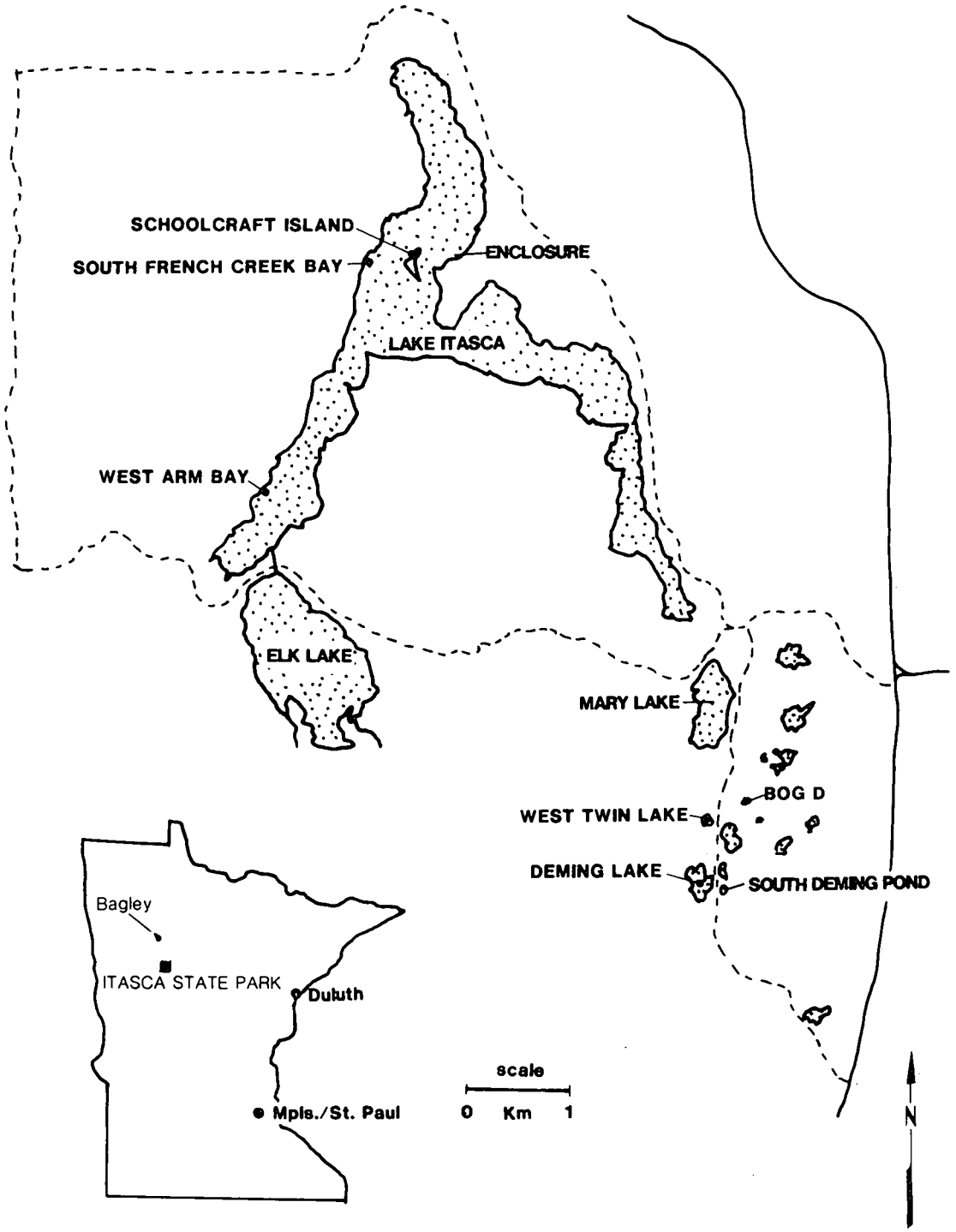
For the purposes of this study, the following terms are predefined: A note is any discrete distribution of sound

shorter/longer than 0.070/0.025 s. Trills consist of a number of very short duration pulses separated from a terminal note by less than 0.05 s. A scream is a long duration, wide frequency band vocalization with no apparent temporal pattern.

The number of each vocalization in a population were censused for five minutes every half hour from 23:30 h to 04:00 h on most nights at West Arm Bay in 1981 and in the enclosure in 1982 (Figure 6).

Playback experiments were performed at a chorus at French Creek Bay from 25 July to 6 August 1982 (Figure 6). A speaker was attached to a 0.5 X 0.5 X 0.03 m piece of styrofoam and floated to 0.75 m from a vocalizing male. This did not appear to disturb the calling male as no change in the number/unit time or type of vocalizations were noted. Frog behaviors (including vocalizations) were recorded continuously in 5 s blocks of time for five minutes prior, during, and after each playback tape. Playback tapes were five minutes in duration and were made from recordings of males outside the French Creek Bay population to control for possible individual identification of neighbors. Sound pressure levels (SPL) of playbacks were set at the level actually noted in the field for that particular vocalization. A Realistic Music/Sound Level Meter at slow needle response was used to measure SPL's. The readings of

Figure 6: Map of Lake Itasca and surrounding lakes in northwest Minnesota: playback experiments were performed at South French Creek Bay


SCHOOLCRAFT ISLAND
SOUTH FRENCH CREEK BAY
ENCLOSURE
LAKE ITASCA
WEST ARM BAY
ELK LAKE
MARY LAKE
BOG D
WEST TWIN LAKE
DEMING LAKE
SOUTH DEMING POND
Bagley
ITASCA STATE PARK
Duluth
Mpls./St. Paul
scale
0 Km 1
N

this instrument may have been up to 10 dB less than those obtained using other brands (Arak 1983). A wooden dowel 0.75 m in length was taped to the meter to permit accurate placement of the meter 0.75 m from calling males. Some (14 out of 210) vocalization sections did not yield discernable amplitude peaks on the sectioner display due to inaccurate pin placement, and were eliminated from sound spectrographic analyses of frequencies.

The SAS (Statistical Analysis System) computer package was used for much of the data analysis (SAS Institute 1982a, 1982b). A few nonparametric methods of Siegel (1956) were used, and a probability of correctly rejecting the null hypothesis of $P<0.05$ was considered statistically significant.

RESULTS

Spectrographic Analysis

Spectrographic analyses are based on 210 sound spectrograms of 27 frogs, an average of 7.78 calls/frog (SD=7.79 calls/frog). Six distinct vocalizations (seven including the alarm scream) are recognized, based on temporal spectrographic differences (Appendix A) and descriptions by previous workers (Peacock and Drake 1971; Carroll 1976; Kelling 1976):

Single Note Calls

Boink: unpredictable single note call, only two calls were recorded with durations of 0.046 s and 0.050 s (Figure 7a).

Cut: single note with a mean duration of 0.027 s (SD=0.006 s, N=16) (Figure 7b). Cuts were significantly shorter in duration than boinks (P=0.027, z=2.21, s=35;, Wilcoxon 2-sample test).

Multiple Note Calls

Series: two- to seven-note sequence of boink notes with a mean call duration of 0.517 s (SD=0.184, N=71) and a mean of 3.423 notes/call (SD=0.889, N=71). The mean note durations for the first five notes were: 0.048 s (SD=0.009, N=71), 0.042 s (SD=0.008, N=71), 0.042 s (SD=0.008, N=71), 0.042 s (SD=0.005, N=71), and 0.037 s (SD=0.002, N=71), respectively (Figure 7c).

Series growl: mean number of 2.292 notes/call (SD=1.169, N=96) combined with a mean number of 3.031 trills/call (SD=1.440, N=96). Mean call duration was 0.979 s (SD=0.243, N=96) (Figure 7d).

Trills Only Calls

Growl: similar to the series growl without the notes. Consisted of trills only, with a mean number of 3.955 trills/call (SD=1.397, N=22) and a mean call duration of 0.885 s (SD=0.347, N=22) (Figure 7e).

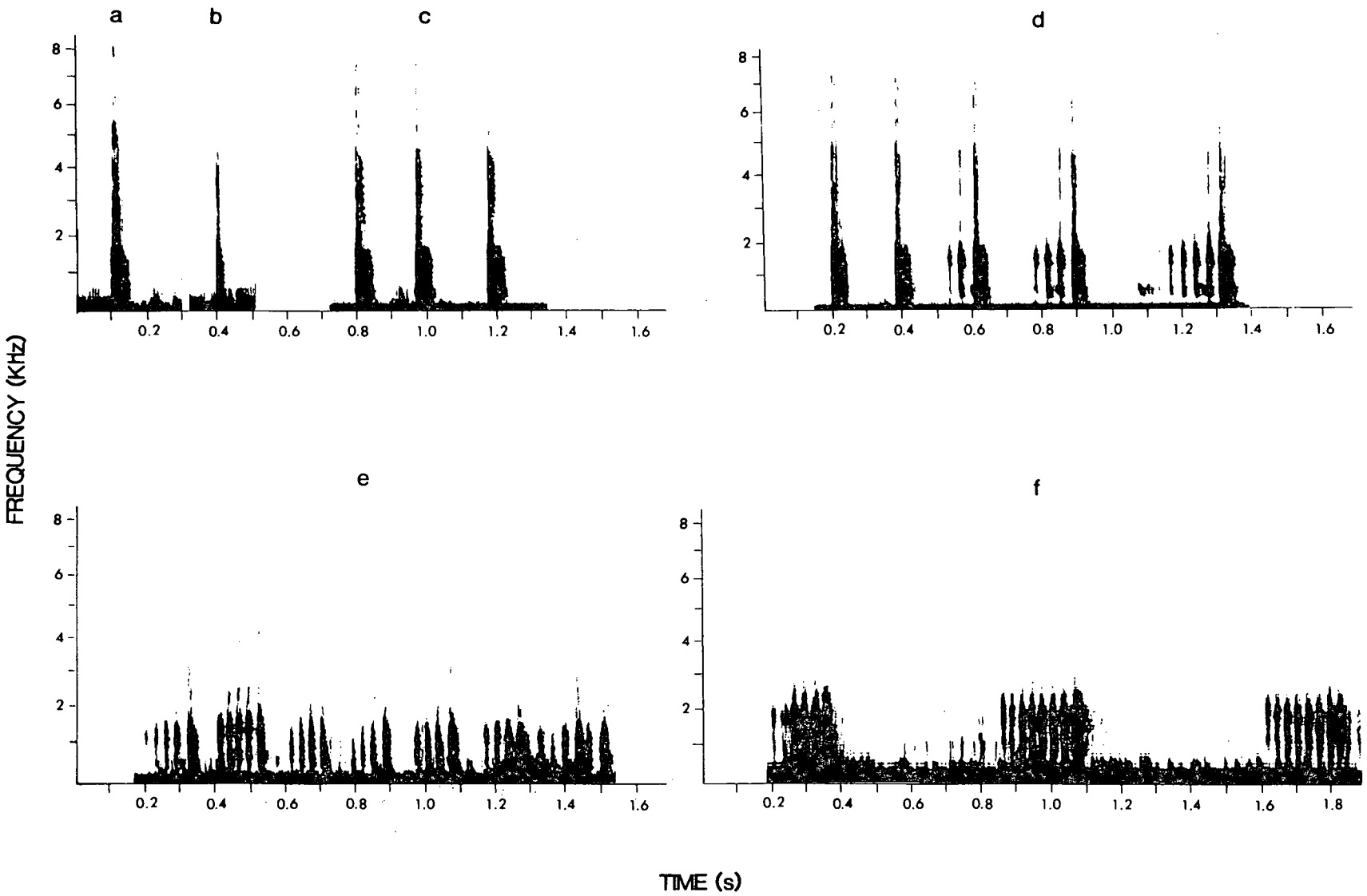
Release growl: very similar to growl. Number of trills/call were 3 and 4 (Figure 7f). Compared to growls, release growls had significantly more pulses in trill one (P=0.025, z=2.25, s=44.50, Wilcoxon 2-sample test), trill two (P=0.020, z=2.33, s=43.00, Wilcoxon 2-sample test), and trill three (P=0.019, z=2.35, s=41.00 Wilcoxon 2-sample test). Also, the duration of the third trill only was longer (P=0.026, z=2.22, s=41.00, Wilcoxon 2-sample test) in release growls than growls.

Scream

Alarm scream: Baird et al. (1972) recorded a wide frequency vocalization, with no distinct temporal pattern, when a female mink frog was being eaten by a water shrew (Blarina brevicauda) (Figure 8).

Males emitted all calls (presuming males emit the scream), and females only emitted the release growl and the scream.

Figure 7: Sound spectrograms of mink frog vocalizations: a=boink, b=cut, c=series, d=series growl, e=growl, f=release growl

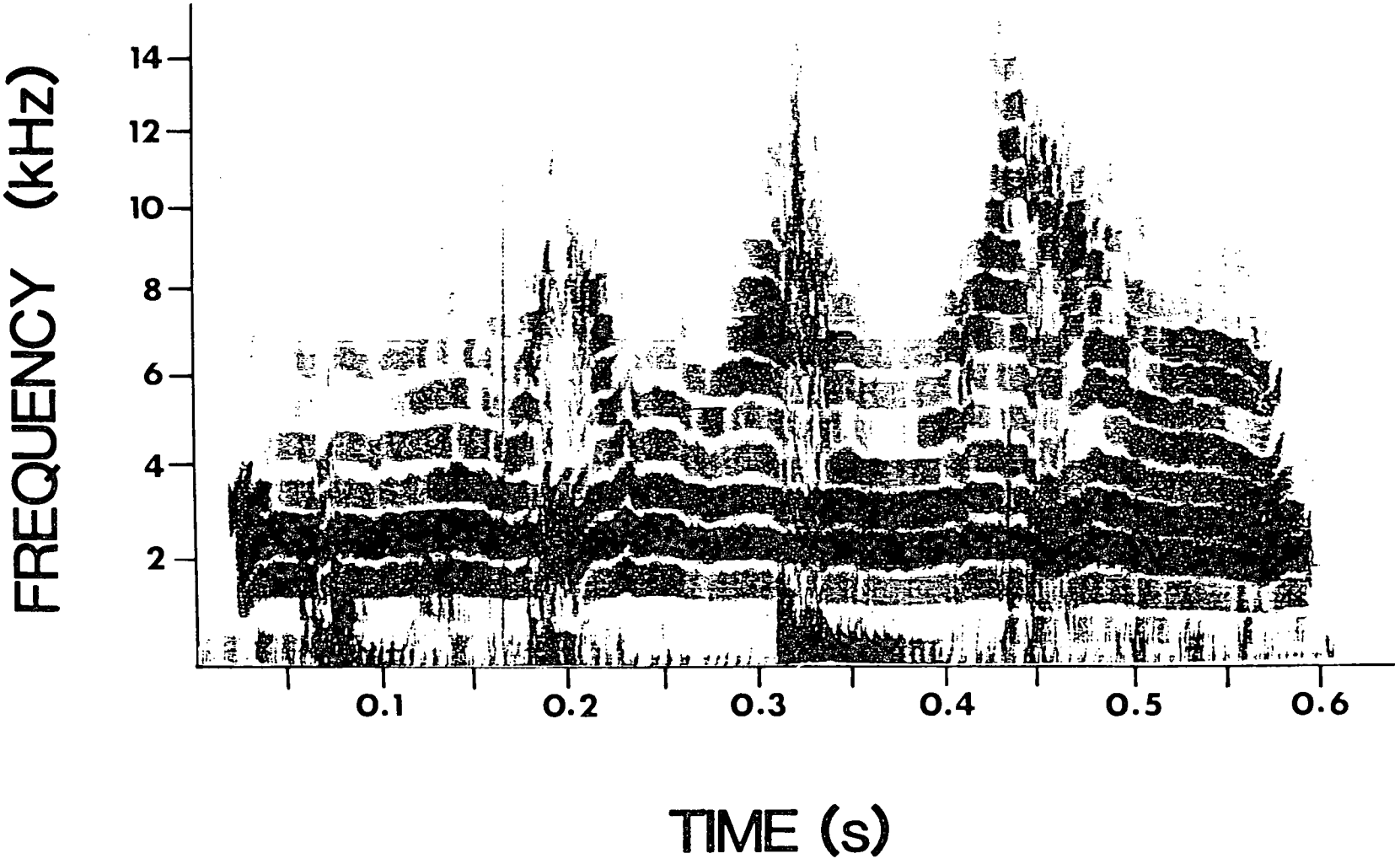

a
b
c
d
e
f
FREQUENCY (KHz)
TIME (s)

All vocalizations consisted of two frequency peaks; a low frequency band of 470-970 Hz and a high frequency band of 1220-1960 Hz. Each vocalization did not consist of significantly different frequency peaks.

There was a significant relationship between mean sound-pressure level (SPL, dB) and vocalization type ($P<0.001$, $H=53.56$ $df=3$, Kruskal-Wallis 1-Way ANOVA). The vocalizations, in descending order of loudness, were: 1) growl ($\bar{x}$= 70.41 dB, SD=0.93 dB, N=10), 2) series growl ($\bar{x}$= 68.96 dB, SD=1.21 dB, N=46), and 3) series ($\bar{x}$= 66.50 dB, SD=1.62 dB, N=36). The change in SPL during growl and series growl vocalizations was not statistically significant.

There was no relationship between male weight or length and 1) dominant call frequency, 2) number of notes/call, 3) amplitude change throughout the call, or 4) call duration ($P>0.05$, Kendall Tau Correlation).

Figure 8: Sound spectrogram of mink frog scream emitted while being eaten by a water shrew (from Baird et al. 1972)


FREQUENCY (kHz)
14
12
10
8
6
4
2
0.1
0.2
0.3
0.4
0.5
0.6
TIME (s)

Playback Experiments

A total of 27 playback experiments were performed during the breeding season on 25 subject frogs ($\bar{x}$= 1.1 trials/frog). The vocal responses of subject animals were recorded in all 27 trials. Movement toward the playback speaker (phonotaxis) was noted in 17 trials (N=17 different subjects); in 10 trials phonotaxic responses were not noted. No males moved away from the speaker. Calling males responded differently to different stimulus calls in distance moved toward speaker (phonotaxic response) (Table 3). Playbacks of boink and series calls evoked the least intense phonotaxic response (Table 3), and series growls, growls, and cuts evoked the strongest phonotaxic responses (Table 3).

The strongest vocal responses occurred during the playback, with post-playback responses the next strongest ($P<0.001$, $G=446.65$, $df=8$, G-test). Vocal responses to stimulus vocalizations were dependent upon the stimulus vocalization. Each type of vocalization presented elicited different vocal responses (Table 4). Table 5 summarizes the playback vocal responses of calling males (N=25 males). Females did not respond to any playback vocalizations.

TABLE 3

Phonotaxic responses of male mink frogs to playbacks (N=17 trials on 17 different individuals)

Distance moved toward speaker (cm)	Stimulus				
	Boink (%)N	Series (%)N	Series growl (%)N	Growl (%)N	Cut (%)N
0-0.24	(60)3	(40)2	(0)0	(0)0	(0)0
0.25-0.47	(0)0	(50)1	(50)1	(0)0	(0)0
0.50-0.75	(0)0	(0)0	(20)2	(40)4	(40)4
contact	(0)0	(0)0	(0)0	(25)1	(75)3

$P<0.01$, $G=28.24$, $df=12$, G-test

TABLE 4

Vocal response during call playbacks for N=27 trials (N=25 calling males)

Response	Stimulus					
	Boink	Series	Series Growl	Growl	Cut	Total
	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)
Boink	0 (0)	2 (2.5)	1 (0.8)	4 (2.9)	0 (0)	7 (1.4)
Series	20 (58.8)	8 (10.1)	15 (12.3)	17 (12.2)	9 (7.2)	69 (13.8)
Series growl	13 (38.2)	28 (35.4)	10 (8.2)	13 (9.4)	8 (6.4)	72 (14.4)
Growl	0 (0)	3 (3.8)	10 (8.2)	7 (5.0)	9 (7.2)	29 (5.8)
Cut	1 (2.9)	38 (48.1)	86 (70.5)	98 (70.5)	99 (79.2)	322 (64.5)
Total	34 (99.9)	79 (99.9)	122 (100.0)	139 (100.0)	125 (100.0)	499 (99.9)

$P<0.0001$, $G=1091.48$, $df=16$; G-test

TABLE 5

Playback responses of 25 calling male mink frogs; B=boink, S=series, SG=series growl, G=growl, C=cut

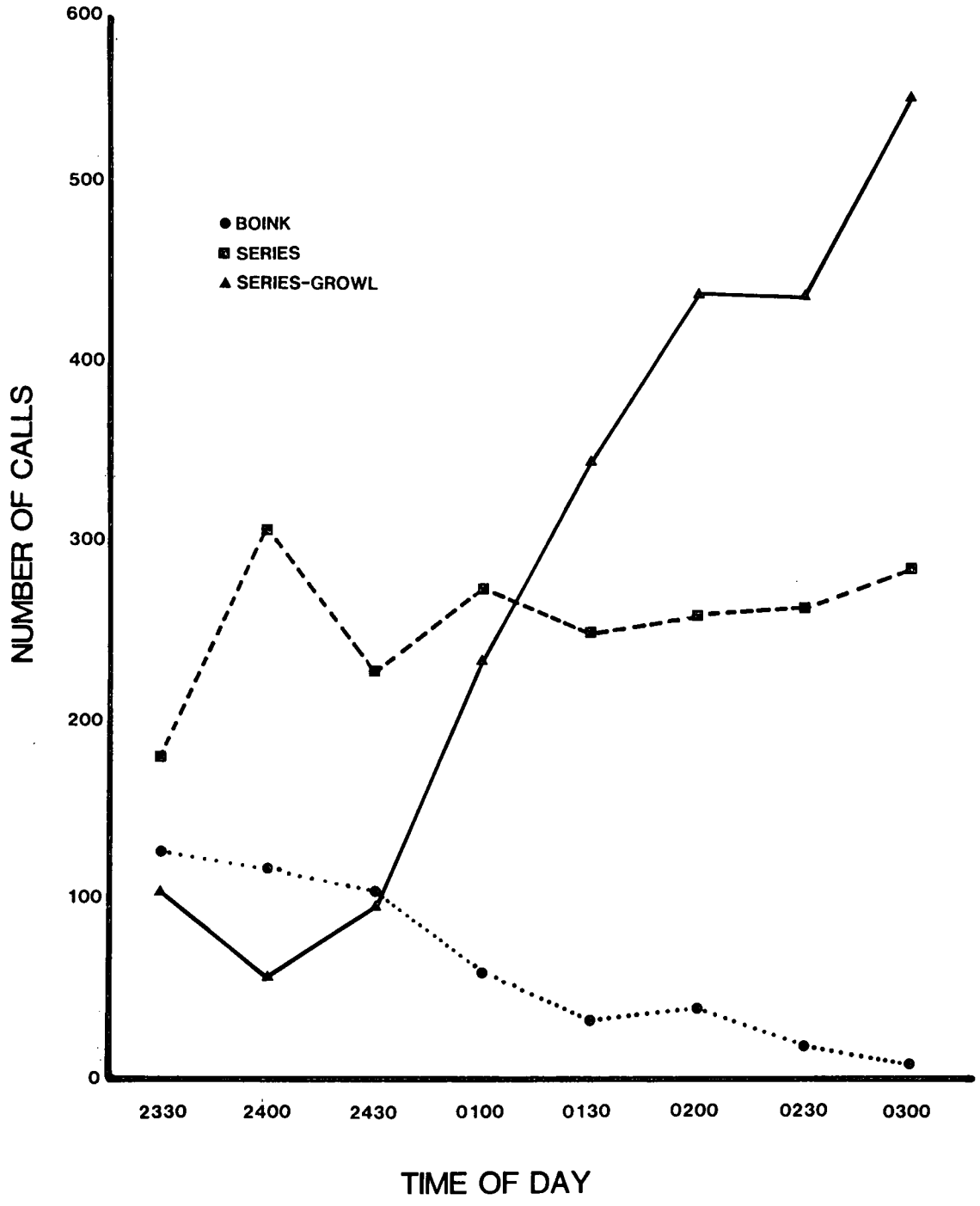
Playback call	Response call (% of total calls)
Boink	S(58.8) SG(38.2) C(2.9)
Series	B(2.5) S(10.1) SG(35.4) G(3.8) C(48.1)
Series growl	B(0.8) S(12.3) SG(8.2) G(8.2) C(70.5)
Growl	B(2.9) S(12.2) SG(9.4) G(5.0) C(70.5)
Cut	S(7.2) SG(6.4) G(7.2) C(79.2)

Context of Vocalizations

The overall distribution over time of boink and series vocalizations were significantly different ($P<0.001$, $d=0.068$, Kolmogorov-Smirnov 2-sample test), as were series and series growls ($P<0.001$, $d=0.060$, Kolmogorov-Smirnov 2-sample test; Figure 9). Boinks peaked at 23:30 h, series at 24:00 h, and series growls at 03:00 h.

Boinks occurred earliest in the evening as males established territories (Figure 9). They were infrequent, peaking (22:30 h) before amplexes or fights occurred. Series occurred prior to amplexes and fights (Figure 9). Territorial males usually uttered these vocalizations when

Figure 9: Observed number of boinks, series, and series growls versus time of day


600
500
400
300
200
100
0
NUMBER OF CALLS
BOINK
SERIES
SERIES-GROWL
2330
2400
2430
0100
0130
0200
0230
0300
TIME OF DAY

distant from other territorial males. Series growls peaked late in the evening at the time of aggressive and mating activities (Figure 9). This vocalization was often given as a counter-call between two or more males in close proximity. Series growls and growls occurred between bouts of fighting. Growls occurred only when males were close together (0-3 m) and were counter-calling or fighting. Growls and cuts occurred late in the evening (usually after 02:00 h). Cuts were only heard during agonistic encounters when males moved. This sound did not carry as far as the other vocalizations. Release growls were heard frequently in the enclosure (1982), emitted from clasped females and occasionally from clasped males (losers of fights).

DISCUSSION

Functional Significance of Mink Frog Vocalizations

A variety of techniques are used to determine the message(s) communicated in vocalizations including context of occurrence (Capranica 1968; Wells 1978; Arak 1983; Odendaal and Bull 1983), the daily temporal pattern of occurrence of calls (Allan 1973), and behavioral (Narins and Capranica 1976; Wells 1978; Rand and Ryan 1981; Gerhardt 1981; Narins 1982; Ramer et al. 1983) and physiological (Brzoska and Obert 1980) responses to playback vocalizations.

Mink frog vocalizations are classified as six distinct calls based on temporal patterns (e.g. number of notes and trills/call). The two single note vocalizations (boink and cut) are distinguishable from each other by call duration. The two vocalizations consisting of trills only (release growl and growl) are distinguishable by different numbers of pulses/trill.

Vocalization temporal pattern appeared to be the cue used by mink frogs to discriminate between calls. Dominant frequency did not vary sigificantly between individuals or calls, nor were there any correlations between male body size and dominant call frequency or duration (in contrast with the green frog, Ramer et al. 1983). Growls were the loudest calls, followed by series growls and series (in decreasing order), which showed significantly different SPL's.

For the multi-note vocalizations, loudness may communicate aggressive motivational state since the loudest calls occur latest at night when males are closest to each other. Upon examining the relative loudness of each call, the time of day of peak occurrence, playback results, and the context of occurrence, the functional significance of each vocalization vocalizations becomes apparent (Table 6).

Boinks and series appear to function as graded advertisement displays (Wells 1977c), communicating

information on species, sex, reproductive state, and location. Series are given by animals that may be in a higher reproductive motivational state than boinks. The series growl may function as a complex call (Wells 1977c), perhaps communicating both advertisement (as above) and threat information (Table 6). The series growl may function in communicating the highly aggressive motivational state of a male and its intentions of territorial defense/takeover, along with advertisement information communicated by the series. Growls appear to function in male aggressive encounters, communicating information about the aggressive motivational state of the male and its intent to fight. Cuts appear to function in the maintenance of auditory contact between interacting males during pre-fight and fight situations. The release growl functions in stimulating the release of a male clasping 1) another male or 2) an unreceptive female.

TABLE 6

Playback response, context of occurrence, and proposed functions of mink frog vocalizations; C=cut, S=series, SG=series growl

Call name	Phonotaxic response	Vocal response	Context	Proposed function
Boink	none	S, SG	early in the evening by widespread territorial males	Advertisement
Series	low	C, SG	peak @ 24:00 h by widespread territorial males	Graded advertisement
Series growl	med	C	peak @ 03:00 h; counter-calls and territorial disputes	Graded advertisement, threat
Growl	high	C	only during intense counter-calling and fights	Threat
Cut	very high	C	only while moving during counter-calling and fights	Threat, indicates location
Release growl	-	-	inappropriate clasp	Elicits release

Comparison of Mink Frog Vocalizations with Green Frog and Bullfrog Vocalizations

The vocal behavior of two close relatives of the mink frog, the green frog and bullfrog (Moore 1949; Case 1978) have been well studied. (Capranica 1968; Emlen 1968; Wiewandt 1969; Wells 1978; Ramer et al. 1983). The dominant call frequencies of green frog vocalizations (500-1000 Hz peak and a 1500-2000 Hz peak) are more similar to mink frog dominant call frequencies (470-970 Hz and 1220-1960 Hz) than the very low, single dominant frequency peak (200-300 Hz or 0-1700 Hz wide band bonk) of the bullfrog.

Based on spectrographic analyses, two green frog vocalizations are similar to three mink frog vocalizations. The green frog type I vocalization (Wells 1978) is structurally similar to the boink and series of the mink frog. The green frog type V call corresponds to the mink frog release growl. There appear to be no great differences between these two calls, except for the longer duration of the type V call. The green frog type I and Type II vocalizations have no counterparts in the mink frog vocal repertoire, but are spectrographically similar (except for frequency distribution) to the bullfrog mating call and bonk call respectively (Wiewandt 1969). The only bullfrog vocalization that is spectrographically similar to any mink

frog vocalizations is the bonk vocalization (Wiewandt 1969). This vocalization is structurally similar to both the cut and boink of the mink frog.

The mink frog boink and series appear to be calls of low aggressive motivation eliciting low aggressive responses from playback subjects. In contrast, the green frog type I vocalization elicits strongly aggressive behaviors from playback subjects (Wells 1978; Ramer et al. 1983). The green frog type IV vocalization appears to be functionally similar to the growl of the mink frog. The major difference between the two is the relative loudness (quietest green frog vocalization, loudest mink frog call). The growl is the loudest of all mink frog vocalizations and consists of a mean of 4.0 trills/call, while the type IV call is the quietest of the green frog vocalizations and consists of one long trill. The bullfrog bonk vocalization appears to functionally similar to the mink frog cut, as it is involved in male-male encounters (Wiewandt 1969). The mink frog vocal repertoire is structurally and functionally more similar to the green frog vocal repertoire than the bullfrog vocal repertoire.

Conclusions regarding functional similarities between these three species' calls are tentative. Neither Wells' (1978) nor Wiewandt's (1969) playback data are quantified. No statistical analyses were performed and only several of

the vocalizations (type III, IV, and V in the green frog; gronk in the bullfrog) were tested for responses to playback calls.

A key in understanding the functional sigificance of a communication system potentially involving mate choice is the response of females to male calls. Mink frog females (N=6) did not respond to any male vocalizations. Choice experiments exposing gravid females to a variety of male vocalizations (perhaps facilitated by pituitary extract injections) would provide insight into this question.

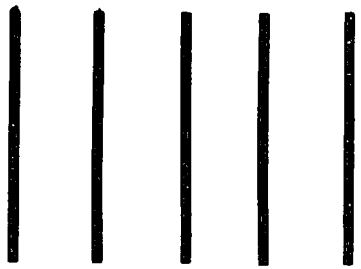
Complex Call

The series growl of the mink frog appears to be a compound advertisement call. Wells (1977c) has defined complex calls as consisting of two distinctly different notes in a single vocalization. Complex calls have been reported for a variety of leptodactylids, hylids, rhacophorids, and pipids (Wells 1977c). The mink frog is the first ranid for which a complex vocalization has been reported. Data from Eleutherodactylus coqui studies (Narins and Capranica 1976) indicate that the two components of the complex call each communicate different information. The advertisement call of E. coqui is composed of an introductory tone-like "co" note followed by a frequency-modulated "qui" note. Females are attracted to the "qui"

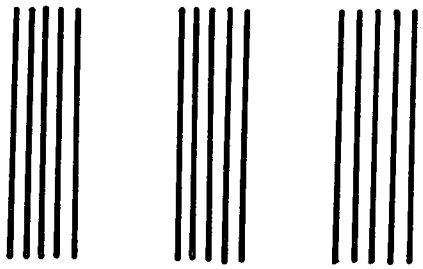
note alone and males respond vocally to the "co" note alone. The "co" note is given alone in agonistic encounters, thus conveying an agonistic message to males while the "qui" note seems to attract females (Narins and Capranica 1976). Wells (1977c) proposed that complex vocalizations evolved from the merging of two independent vocalizations. This seems to be the situation with the mink frog series growl (Figure 10). When comparisons are made between male responses to series playbacks (little phonotaxic response), growl playbacks (high phonotaxic response), and series growl playbacks (moderate phonotaxic response), it is apparent that the responsiveness of males varies with the presense of series notes (courtship) and trills (aggression). If this call is analogous to the E. coqui call, then females are attracted by the series portion of the series growl, and males respond aggressively to the growl portion of the series growl. The responses of females to playbacks are critical in determining the functional significance of any calls in terms of courtship.

Apparently notes and trills, being common to the three ranids compared, are primitive in evolutionary origin. The combination of these two call types to form a "new" call (series growl) suggests it is more recently evolved.

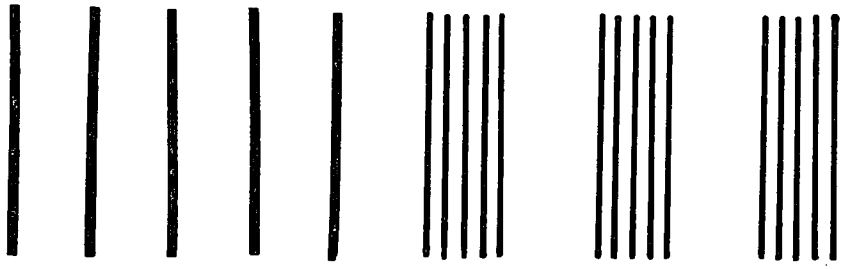
Figure 10: Proposed developmental sequence of the mink frog *series growl* vocalization



SERIES



GROWL



SERIES GROWL

SUMMARY

Sound spectrograms were made from 210 recorded mink frog calls (N=27 calling males). All vocalizations consisted of sound energy peaks at 470-970 Hz and 1220-1960 Hz. Calls were classified into six distinct categories based on temporal pattern differences: 1) boink (long duration single note), 2) cut (short duration single note), 3) series (multiple boink notes), 4) series growl (combination of boink notes and trills), 5) growl (multiple short duration trills), and 6) release growl (multiple long duration trills).

Growls were the loudest vocalizations (mean SPL=70 dB), followed by series growls (mean SPL=69 dB), and series (mean SPL=67 dB). For these vocalizations, SPL may have been used to communicate the aggressive motivational state of the animal. Loud vocalizations may have indicated highly aggressive animals.

Boinks and series appear to function as graded advertisement displays, with series uttered by more sexually motivated animals. Series growls may function as compound advertisement calls, communicating aggressive as well as courtship information. Series growls are probably derived from the merging of series and growl calls. Growls appear

to communicate a male's willingness to fight and cuts communicate the spatial locations of interacting males. Release growls function in the same manner as most other anuran release calls; by stimulating the clasping male to release its grasp of an unsuitable mate. The series growl is the first compound advertisement vocalization reported for the family Ranidae.

The mink frog bimodal call dominant frequency (470-970 Hz- 1220-1960 Hz) is more similar to that of the green frog (500-1000 Hz and 1500-2000 Hz) than the bullfrog's (200-300 Hz). Temporal/functional characteristics of mink frog vocalizations resemble those of the green frog more closely than those of the bullfrog. The vocabulary of the mink frog appears to be more recently derived than the green frog's or bullfrog's, as evidenced by the compound advertisement call of the mink frog.

DECLINE OF THE MINK FROG IN MINNESOTA

INTRODUCTION

The mink frog (Rana septentrionalis), a small- to medium-sized member of the anuran family Ranidae (46 genera, 560 species worldwide; one genus, 21 species in North America), ranges from Labrador to northern New Hampshire and westward to northeastern Minnesota and southeastern Manitoba. The northern limits of its range are unknown (Hedeen 1977).

The mink frog is one of the most nocturnal and aquatic North American ranids (Marshall and Buell 1955; Schmid 1965). This species inhabits areas of slow moving water with dense vegetative cover (Breckenridge 1944; Hedeen 1970), and is found away from water only during rainstorms when individuals sometimes move between bodies of water (Hedeen 1970).

The mink frog oviposits during mid-June to early August (Breckenridge 1944). The tadpole stage lasts 1-2 y, and tadpoles metamorphose from 24 June to 30 August (Wright and Wright 1949; Hedeen 1971) at 29 to 42 mm snout-vent length (SVL) (Hedeen 1977). Females reach maturity at a larger size (54-59 mm) than males (45-50 mm) (Hedeen 1972a).

Hedeen (1972a) used a "sex-index" (Martof 1956) based on SVL/tympanum diameter to sex mink frogs in the field. This technique was verified by internal examination of the gonads and was found to be accurate for frogs longer than 48 mm (SVL) 98% of the time (Hedeen 1972a). Mink frogs were sexed as: 1) males if the sex-index was less than 10 and the SVL was at least 48 mm, 2) females if the sex-index was at least 10 and the SVL was at least 48 mm, and 3) juveniles if the SVL was less than 48 mm.

At Itasca State Park, mink frogs are first observed on warm days during spring (April-May). On cool days the frogs remain underwater. Reproductive activity occurs from late June to early August (Hedeen 1972a). With the onset of cool weather in fall, adults and juveniles move to overwintering sites in deep water and spend only warm days at the water's surface (Hedeen 1970). The mink frog may not hibernate, as it has been captured under the ice mid-winter in minnow traps (J.C. Underhill pers comm).

Due to the difficulty of finding dense groups of calling males for behavioral ecology studies, an investigation of the distribution and abundance of the mink frog in Itasca State Park was undertaken. Several unpublished reports by students at the University of Minnesota Forestry and Biological Station (Lemmerman and White 1958; MacDonald and Engebretson 1959; McKenzie 1962;

Wunderle and Wenstrom 1970; Peacock and Drake 1971; Priemer et al. 1973; Caponi 1976) and Hedeen's (1970) PhD Dissertation were used to determine past population trends and locate appropriate study areas. Observations prior to 1981 suggested a marked decline of mink frogs in the Park. A decline since the early 1970's was reported in Wisconsin (Hine et al. 1981) and Minnesota (McKinnell et al. 1979) for the leopard frog, Rana pipiens.

Specific objectives of this study are to 1) determine the current abundance of mink frogs at sites previously studied, and 2) compare current estimates with those of previous workers to estimate mink frog population trends.

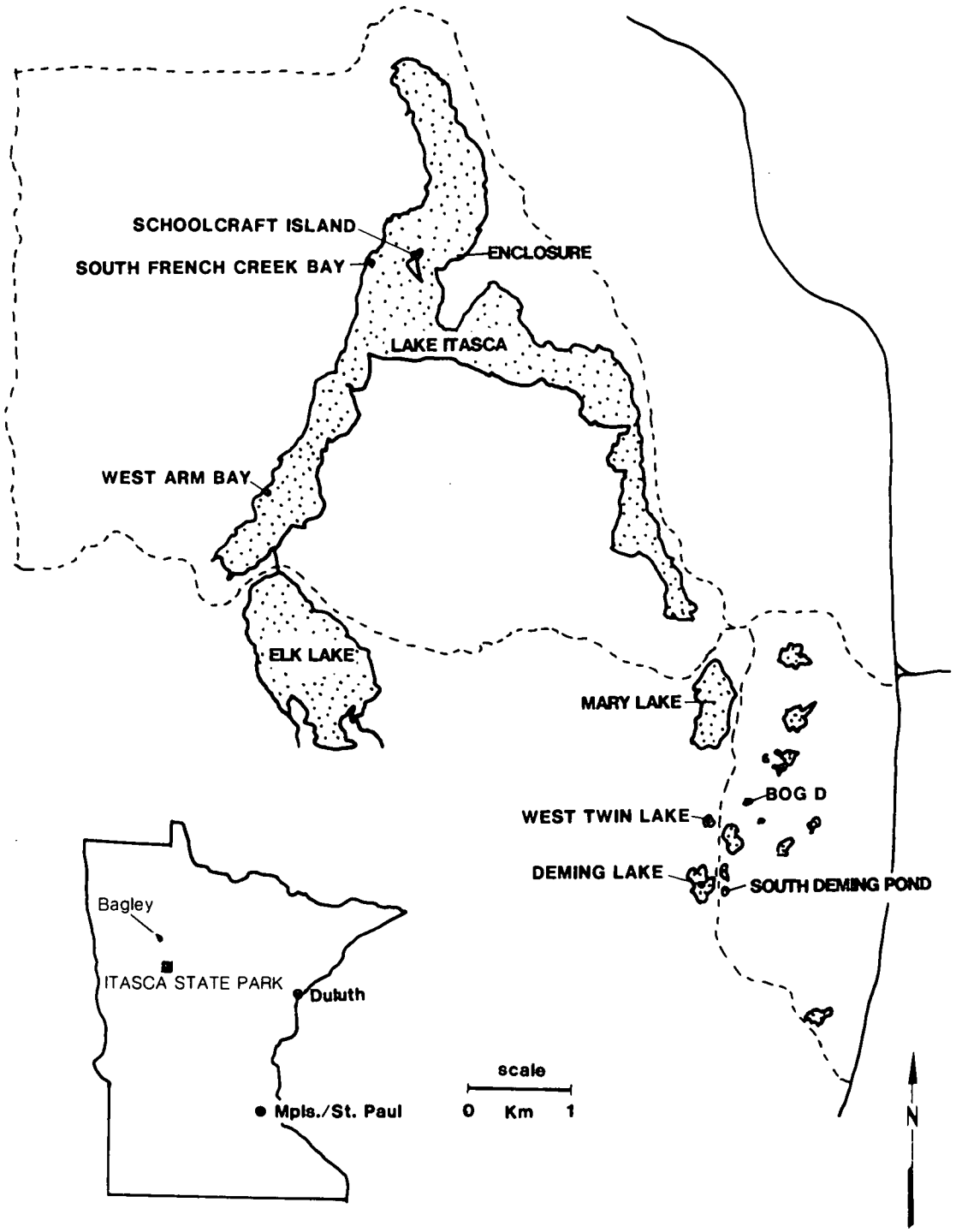
MATERIALS AND METHODS

The study was initiated on 18 June 1982 and was terminated on 27 August 1982 in Itasca State Park in northwestern Minnesota. This area was chosen for study because it consisted of the same area as an ongoing behavioral ecology project. Mark-recapture data were gathered on 24 nights. Few samples were taken in July due to a conflict with a concurrent behavioral ecology project (Chapters I and II). Twelve initial sites were chosen to compare with previous population estimates in the literature (Appendix B). Of these, five were eliminated because of low mink frog population densities or extreme vegetation density

precluding the use of a canoe. The six mark-recapture study sites chosen were Bog D, Deming Lake, Schoolcraft Island, South French Creek Bay, West Arm Bay, and West Twin Lake (Figure 11). In addition to these six, the population size of South Deming Pond was estimated by total removal; the captured frogs were used to stock an enclosure on Lake Itasca (Chapter I).

Each area was sampled in random order once every three to four nights. Investigators used headlamps and hand-lanterns to help locate frogs, which were captured by hand. All frogs were toe-clipped using a technique similar to that used by Martof (1956). Snout-vent length (with the animal pressed flat) was measured to the nearest 1 mm. Tympanum diameter was measured to the nearest 0.1 mm. Frogs were weighed using a Pesola 50 g scale and plastic bag to the nearest 0.25 g. Handling time was 1-2 min per frog and animals were released immediately after being weighed. Individuals were sexed in the manner of Hedeen (1972a). The methods of Seber (1973) were used to determine population densities based on multiple recapture data (Schnabel Index). The SAS (Statistical Analysis System) computer package was used for much of the statistical analysis (SAS Institute 1982a, 1982b). A few nonparameteric methods of Siegel (1956) were used, and a probability of correctly rejecting the null hypothesis of $P<0.05$ was considered statistically significant. Comparative population data were obtained from

Figure 11: Map of the six sites in Itasca State Park chosen for mark-recapture studies in 1982


SCHOOLCRAFT ISLAND
SOUTH FRENCH CREEK BAY
ENCLOSURE
LAKE ITASCA
WEST ARM BAY
ELK LAKE
MARY LAKE
BOG D
WEST TWIN LAKE
DEMING LAKE
SOUTH DEMING POND
Bagley
ITASCA STATE PARK
Duluth
Mpls./St. Paul
scale
0 Km 1
N

several class reports from the University of Minnesota Forestry and Biological Station (Lemmerman and White 1958; MacDonald and Engebretson 1959; McKenzie 1962; Peacock and Drake 1971; Priemer et al. 1973; Caponi 1976).

RESULTS

A total of 314 mink frogs were captured. Of these, 47 (15%) were adult males, 64 (21%) were adult females, and the rest (193 or 63%) were juveniles. Ten males were captured as the result of non-random sampling and were eliminated from the following considerations.

The sex ratio of all captured adults was 1.0:1.4 (males:females). The sex ratio varied from a low of no males at Bog D, Schoolcraft Island, West Arm Bay, and West Twin Lake to a high of 5.0:1.0 at Deming Lake (Table 7). Also, the frequency of each sex-age class (males, females, juveniles) varied between capture sites significantly (Table 7).

Table 12 shows population estimates and confidence intervals for those study sites (Deming Lake, South French Creek Bay, West Arm Bay, West Twin Lake) where recapture numbers were high enough to calculate Schnabel Indices (Seber 1973). Deming Lake had the largest population (178) and West Arm Bay had the smallest (16).

TABLE 7

Number of each sex-age class captured at each study site; BD =Bog D, DL=Deming Lake, SI=Schoolcraft Island, SDP=South Deming Pond, SFCB=South French Creek Bay, WAB=West Arm Bay, WTL=West Twin Lake

	Capture site						
Sex	BD	DL	SI	SDP	SFCB	WAB	WTL
Males	0	20	0	10	14	0	0
Females	7	4	1	22	19	2	2
Juveniles	9	97	11	0	25	8	43
Total	16	121	12	32	58	10	45

$P<0.001$, $G=181.99$, $df=12$, G-test

TABLE 8

Schnabel population estimates with 95% confidence intervals for four study sites

Study site	N (est)	95% Confidence intervals	
Deming Lake	178	134	257
South French Creek Bay	27	19	37
West Arm Bay	16	3	46
West Twin Lake	42	23	61

Mean weight (Table 9) and mean snout-vent length (SVL) (Table 10) varied significantly between study sites for males and juveniles, but not females.

TABLE 9

Mean (and standard error of the mean: SE) weights for males, females, and juveniles for each study site in Itasca State Park; BD=Bog D, DL=Deming Lake, SI=Schoolcraft Island, SDP=South Deming Pond, SFCB=South French Creek Bay, WAB=West Arm Bay, WTL=West Twin Lake

	Males*		Females**		Juveniles***	
Study site	Mean	SE	Mean	SE	Mean	SE
BD	-	-	11.82	3.10	4.72	1.88
DL	15.15	0.71	15.56	3.54	7.55	0.22
SI	-	-	9.00	-	8.80	0.22
SDP	14.14	1.61	19.47	0.86	-	-
SFCB	18.69	1.51	18.88	2.17	7.54	0.49
WAB	-	-	19.50	2.50	10.32	0.65
WTL	-	-	15.38	0.13	6.90	0.69

*P<0.001, H=15.87, df=2, Kruskal-Wallis 1-Way ANOVA
**P>0.05, Kruskal-Wallis 1-Way ANOVA
***P=0.008, H=15.60, df=5, Kruskal-Wallis 1-Way ANOVA

Redleg symptoms (reddish discoloration of the ventral portion of the limbs and body) (Emerson and Norris 1905), attributed to the bacterium Aeromonas hydrophila, was found in 19% of all captured frogs. Juveniles showed signs of

TABLE 10

Mean (and standard error of the mean: SE) snout-vent lengths (SVL) for males, females, and juveniles for each study site; BD=Bog D, DL=Deming Lake, SI=Schoolcraft Island, SDP=South Deming Pond, SFCB=South French Creek Bay, WAB=West Arm Bay, WTL=West Twin Lake

	Males*		Females**		Juveniles***	
Study site	Mean	SE	Mean	SE	Mean	SE
BD	-	-	59	2	49	1
DL	56	1	56	3	43	0
SI	-	-	54	-	46	1
SDP	52	6	63	1	-	-
SFCB	61	1	63	1	42	1
WAB	-	-	62	6	46	1
WTL	-	-	55	2	44	2

*P=0.003, H=11.64, df=2, Kruskal-Wallis 1-Way ANOVA
**P>0.05, Kruskal-Wallis 1-Way ANOVA
***P<0.001, H=42.58, df=5, Kruskal-Wallis 1-Way ANOVA

redleg more often than either adult sex ($P<0.025$, $G=7.97$, $df=2$, G-test). Small frogs (based on snout-vent length) were not affected significantly more often than large frogs ($P>0.05$, Mann-Whitney U-test). Of the three sex-age classes, only females showed a significant difference in the proportion of affected individuals between study sites ($P<0.05$, $G=14.212$, $df=6$, G-test).

DISCUSSION

Comparisons of current population estimates with those of previous workers is found in Table 11. Mink frog population declines (of up to an order of magnitude: Schoolcraft Island and West Twin Lake) were noted at all sites investigated. A portion of the observed decline at Schoolcraft Island may have been due to the removal of mink frogs from that site. A total of 100 adults were removed from the island in 1959 (MacDonald and Engebretson 1959), and in 1962 71 adults were taken (McKenzie 1962). However, the Schoolcraft Island population appeared to recover as evidenced by relatively high population levels in the late 1960's. Other sites investigated, to the best of my knowledge, were not subjected to removal of adults from the area.

A 50% decline in leopard frog numbers occurred in the United States during the 1960's (Hine et al. 1981; Hird et al. 1981). Only 16% (1975) and 28% (1976) of suitable habitat sites were occupied by leopard frogs in Wisconsin (Hine et al. 1981). Many formerly good breeding areas in Wisconsin were not used by leopard frogs, and one area (East Central Study Area) studied by Hine et al. (1981) yielded spring population estimates from 2 to 76 leopard frogs in 1975 and 1976. This contrasted with populations of 124 to 1568 during the 1950's and early 1960's in similar areas of Minnesota (Merrell 1968).

TABLE 11

Population data for sites on and around Lake Itasca from the literature and current study; BD=Bog D, SI=Schoolcraft Island, SFCB=South French Creek Bay, WTL=West Twin Lake, N=number estimated, T=total number observed, A=number of adults of an unknown sex observed, M=number of adult males observed, F=number of adult females observed, J=number of juveniles observed

Site	Year	N	T	A	M	F	J	Method of estimate	Source
BD	1967		40	23			17	# sighted along 300′ transect	Hedeen 1970
	1982						4	# sighted along 300′ transect	present study
	1982					9	7	total #	present study
SI	1955	162						Schnabel Index	MacDonald and Engebretson 1959
	1956	176						Schnabel Index	MacDonald and Engebretson 1959
	1958	94			56	39		Schnabel Index	Lemmerman and White 1958
	1959		122		50	50	22	total # observed	MacDonald and Engebretson 1959
	1962		71		35	36		total # observed	McKenzie 1962
	1969	90						Schnabel Index	Wunderle and Wenstrom 1970
	1970	71						Schnabel Index	Wunderle and Wenstrom 1970
	1971		21					total # observed	Peacock and Drake 1971
	1981				2	2		total # observed	present study
	1982					1	11	total # observed	present study
SFCB	1970		50-					total #	Hedeen 1970
	1973		4-5					total # per unit shoreline	Priemer et al. 1973

TABLE 11 CONTINUED

Site	Year	N	T	A	M	F	J	Method of estimate	Source
	1976		16		11	5		total # observed	Caponi 1976
	1982	27	58		14	19	25	Schnabel Index	present study
WTL	1966		242					total # observed	Hedeen 1970
	1967		1480					total # observed	Hedeen 1970
	1982		42			2	43	Schnabel Index	present study

Several factors have been proposed as possible causes of frog population declines. These include loss of wetland habitat (Cooke 1972), toxicity due to pesticides and other chemicals (Hine et al. 1981), and redleg disease (Anonymous 1973). The Lake Itasca region is part of the Minnesota State Park system and, to the best of my knowledge, no wetlands within the park have been drained. Loss of wetland habitat is probably not a significant factor in the decline of mink frog populations in the Park. Leopard frog population declines in Wisconsin are thought to have resulted from the effects of chemicals (Hine et al. 1981). Periodic administrations of herbicides have occurred in parts of the Park. In the late 1950's, 2-4-5-T was used to eliminate brush from turnout vistas along the East edge of

Lake Itasca. Runoff from these areas would have carried the herbicide into Lake Itasca. In the early 1970's, a pine regeneration area was sprayed with herbicides to facilitate pine growth. Herbicides may have been carried by runoff into an adjacent sewage lagoon. This same sewage lagoon was later (mid-1970's) sprayed to control cattails, Typha sp. Some herbicides may have then entered Lake Itasca via Bear Paw Creek, which runs between the sewage lagoon and the lake (supposedly isolated from each other by a clay dam). Recently (summers of 1982-3), the boat marina on the East shore of Lake Itasca was treated with an herbicide to remove aquatic vegetation. With the above exceptions, no other sites within the Park have been sprayed (B. Toma, Park Naturalist, pers. comm.). Toxic chemicals may have had an effect on populations of mink frogs on Lake Itasca, but could not have affected populations away from the lake that were not subjected to herbicide spraying. Because the mink frog decline is so widespread, even in areas where no spraying of chemicals occurred, it is unlikely that toxic chemicals played an important role in the decline of mink frog populations in the Park.

One possibility, not yet investigated, is the potential for an epidemic spread of an unidentified virus. This possibility can only be refuted/substantiated with laboratory techniques beyond the scope of this study.

The aquatic bacterium, A. hydrophila, has been identified as an important source of mortality in anurans. Captive animals infected with A. hydrophila invariably die within several days unless isolated and maintained at cold temperatures (Emerson and Norris 1905). It is not known what proportion of frogs infected in the wild die. In studies of leopard frogs Hird et al. (1981) found that A. hydrophila could be isolated from both healthy appearing and obviously ill frogs, indicating that the proportion of infected individuals may have been much higher than the number of animals showing symptoms of redleg. They also reported that the degree of infestation was related to overwintering, such that animals that overwintered were most susceptible to the disease. It was proposed that A. hydrophila was present in the water at all times, and that the combined stress of overwintering and carrying the bacterium may have contributed to leopard frog mortality.

Redleg symptoms were found in 19% of all mink frogs captured, and symptoms occurred more frequently in juveniles than either adult sex. The data reported here for mink frogs contrasted with those of Hird et al. (1981), where it was reported that newly metamorphosed frogs (juveniles) were least affected by A. hydrophila. The Lake Itasca region does experience severe winter conditions, and redleg may contribute to overall patterns of mink frog mortality, along with other factors such as low $[O_2]$ resulting from long, severe winter conditions.

There are several possible explanations for the observed sex ratio of 1.0:1.4. First, the observed sex ratio may be biased due to sampling error. Males were found more often in deeper water (resting or calling) than females or juveniles which were found most frequently in dense vegetation near shore. The variability of vegetative cover between study sites may have resulted in one or the other sex having a greater probability of capture. This, however, did not seem to be the case as careful searches were made at all the sites. If anything, males should have been easiest to capture, thus artificially biasing the sex-ratio toward males.

An explanation for the female-skewed sex ratio proposed by Hedeen (1970) assumes that territorial males are more susceptible to predation than females. Hedeen (1972b) observed great blue herons (Ardea herodias) feeding on mink frogs, but had no data indicating that males were taken preferentially over females. Male mink frogs are sometimes active throughout the day during the breeding season (late June through early August). Active males are likely to attract the attention of diurnal/nocturnal predators while establishing or maintaining territories (fighting and vocalizing). Active, territorial male bullfrogs (Rana catesbiana) were the most common category of bullfrog predated by snapping turtles (Chelydra serpentina) (Howard 1978a) at night. A similar situation may be in effect for

the mink frog. Large fish are potential predators of mink frogs, but fish appear to find them distasteful (Oring pers comm 1981).

Hedeen (1970) found that the sex-age classes (juveniles, females, males) exhibited different movement patterns during the post-breeding season (mid-August until first ice). Most males remained at the breeding sites, although a few dispersed to other aquatic habitats. Females usually occupied shallow non-breeding habitats, and juveniles were much less predictable in habitat preference. Juveniles were observed to emigrate in large numbers from Deming Lake in 1967, although no corresponding emigration occurred at West Twin Lake. Based on these observations, Hedeen proposed several possible stimuli for differential juvenile migration between lakes, indicating that juveniles prefer areas of low population density, abundant food, and little open (non-vegetated) water. These potential differences in habitat preferences, that relate to sex-age classes, may contribute to the inequality in observed sex ratios between study sites.

SUMMARY

Mink frog numbers declined at all sites censused. At two sites, Schoolcraft Island and West Twin Lake, population numbers declined by an order of magnitude over a period of 25 and 15 y, respectively.

Several factors including loss of wetland habitat, toxicity due to pesticides, and redleg disease have been implicated in frog population declines. Because the subject mink frog populations were within the bounds of Itasca State Park, and the decline was widespread and included several different populations in areas that were not sprayed with herbicides, loss of wetland habitat and pesticide toxicity were not considered to have an important effect. The possibility of an epidemic viral infection was introduced, but no evaluation of its probability of occurrence was made.

Nineteen percent of all captured mink frogs showed signs of the disease redleg. The actual number of infected frogs may have been much higher since many healthy appearing leopard frogs were shown to carry the agent of the disease, Aeromonas hydrophila (Hird et al. 1981). The symptoms of redleg were found to affect females only differently between study sites. Juveniles showed signs of the disease significantly more frequently than either adult sex. This was contrasted with the leopard frog, in which newly metamorphosed frogs showed the lowest degree of infection

(Hird et al. 1981). Redleg was thought to be at most a secondary cause of the observed mink frog population decline. Perhaps the combined effect of carrying redleg disease and severe winters (low dissolved $[O_2]$) were the source of mink frog mortality.

The overall sex-ratio was female-skewed. This may have been due to differential predation of males based on high levels of male activity during the beeding season combined with female behavioral crypsis. Different proportions of the sex-age classes between study sites may have resulted from different habitat preferences and movement patterns.

GENERAL SUMMARY

Mink frogs of both sexes inhabit the shallow littoral zone during the day. At sunset, males move into deep water territories. Deep water may be a requirement for oviposition sites as egg masses are found under the surface of the water (Wright and Wright 1949; Hedeen 1970).

Males at West Arm Bay, Lake Itasca, chorused from 24 June to 17 August 1981 and from 22 June to 15 August 1982. Because of this long chorus duration and the long period of female ovulation (15 June to 30 July, McKee 1962), mink frogs are classified as "prolonged" as opposed to "explosive" breeders (Wells 1977b).

Even though males did not spend more days at the breeding chorus than females, the operational sex ratio (OSR) was skewed toward males based on the low number of reproductively ready females present on any given day (females are fertile for only several days, McKee 1962).

Only 28% (4/14) of all males were territorial in 1981. Those males that were territorial defended one territory for the duration of the season, but utilized a mean of 9.75 calling sites within that territory. Males were site tenacious, and some sites appeared to be preferred over

others as evidenced by the aggressive displacement of the resident and subsequent occupation of a site by a male.

Both sexes were non-randomly distributed throughout West Arm Bay (1981). Calling males were spaced significantly farther apart than non-calling males, and non-calling males were spaced farther apart than females. Based on a mean nearest-neighbor distance of 9.3 m for calling males, the mean circular mink frog territory size was estimated to be 272 m^2.

Over half (59%) of all aggressive encounters were vocal, in the form of counter-calling. The rest involved overt physical aggression, consisting of jump attacks, head-butting, wrestling, clasping, and chases. Heavy males won significantly more fights than light males, and losing males adopted low, unobtrusive postures in the water. Male amplexus success was highly variable ($\bar{x}$= 1.3 females, SD=4.24), but no relationships between male characteristics and amplexus success were isolated.

Female mink frogs were neither aggressive nor territorial. They were behaviorally cryptic at all times of the day and on four occasions were observed to move unobtrusively through the breeding chorus. The events of a mink frog amplexus were described in the wild for the first time. The locations of one complete and one partial egg mass were within the amplexing male's territory, as was

demonstrated for the green frog and bullfrog. The mating system was described as a resource defense polygyny based on Emlen and Oring's (1977) classification.

Mating behavior of the mink frog was similar to that of the green frog and bullfrog, with several exceptions:

1) Mink frog territory size at low population densities was larger than green frog and bullfrog territory size. At higher mink frog densities, however, mink frog territory size was comparable to those of the green frog and bullfrog.

2) Mink frog wrestling bout durations were similar to those of the green frog, and both were shorter than those of the bullfrog.

3) Mink frogs did not appear to use vocal pouch visual displays during male-male aggressive interactions, in contrast to the green frog and bullfrog.

4) Mink frogs did not utilize jumping and loud splashing displays to advertise territory location, again contrasting with both the green frog and bullfrog.

Sound spectrograms were made from 210 recorded mink frog calls (N=27 calling males). All vocalizations

consisted of sound energy peaks at 470-970 Hz and 1220-1960 Hz. Calls were classified into six distinct categories based on temporal pattern differences: 1) boink (long duration single note), 2) cut (short duration single note), 3) series (multiple boink notes), 4) series growl (combination of boink notes and trills), 5) growl (multiple short duration trills), and 6) release growl (multiple long duration trills).

Growls were the loudest vocalizations (mean SPL=70 dB), followed by series growls (mean SPL=69 dB), and series (mean SPL=67 dB). For these vocalizations, SPL may have been used to communicate the aggressive motivational state of the animal. Loud vocalizations may have indicated highly aggressive animals.

Boinks and series appear to function as graded advertisement displays, with series uttered by more sexually motivated animals. The series growl may function as a compound advertisement call, communicating aggressive as well as courtship information, and is the first such vocalization reported for a ranid. Series growls are probably derived from the merging of series and growl calls. Growls appear to communicate a male's willingness to fight and cuts communicate the spatial locations of interacting males. Release growls function in the same manner as most other anuran release calls; by stimulating the clasping male to release its grasp of an unsuitable mate.

The mink frog bimodal call dominant frequency (470-970 Hz- 1220-1960 Hz) is more similar to that of the green frog (500-1000 Hz and 1500-2000 Hz) than the bullfrog's (200-300 Hz). Temporal/functional characteristics of mink frog vocalizations resemble those of the green frog more than those of the bullfrog. The vocabulary of the mink frog appears to be more highly derived than the green frog's or bullfrog's, as evidenced by the compound advertisement call of the mink frog.

Mink frog numbers declined at all sites censused. At two sites, Schoolcraft Island and West Twin Lake, population numbers declined by an order of magnitude over a period of 25 and 15 y, respectively.

Several factors including loss of wetland habitat, toxicity due to pesticides, and redleg disease have been implicated in frog population declines. Because the subject mink frog populations were within the bounds of Itasca State Park, and declines occurred in areas of the Park where no herbicides were sprayed, loss of wetland habitat and pesticide toxicity were not considered to have an important effect. The possibility of a viral epidemic was introduced, but its potential effects were not evaluated.

Nineteen percent of all captured mink frogs showed signs of the disease redleg. The actual number of infected frogs was probably much higher because many healthy

appearing leopard frogs were shown to carry the agent of the disease, Aeromonas hydrophila (Hird et al. 1981). The symptoms of redleg were found to affect females only differently between study sites. Juveniles showed signs of the disease significantly more frequently than either adult sex. This was contrasted with the leopard frog, in which newly metamorphosed frogs showed the lowest degree of infection (Hird et al. 1981). Redleg was thought to be at most a secondary cause of the observed mink frog population decline. Perhaps the combined effect of carrying redleg disease and severe winters (low concentrations of dissolved O_2) were the source of mink frog mortality.

The overall sex-ratio was female-skewed. This may have been due to differential predation of males based on high male activity during the beeding season combined with female behavioral crypsis. Different proportions of the sex-age classes between study sites may have resulted from different habitat preferences and movement patterns.

Appendix A

TABLE 12

Mink frog call parameters used in sound spectrographic analysis

Variable	Call name					
	B	S	SG	G	C	RG
	M SE	M SE	M SE	M SE	M SE	M SE
Call duration (s)	0.048 0.002	0.517 0.022	0.979 0.025	0.885 0.076	0.027 0.001	1.476 0.132
Number of notes	1.0 0.0	3.4 0.022	2.3 0.119	0.0 0.0	1.0 0.0	0.0 0.0
Note 1 duration (s)	- -	0.048 0.001	0.045 0.001	- -	- -	- -
Note 2 duration (s)	- -	0.042 0.001	0.042 0.001	- -	- -	- -
Note 3 duration (s)	- -	0.042 0.001	0.043 0.002	- -	- -	- -
Note 4 duration (s)	- -	0.042 0.001	0.045 0.005	- -	- -	- -
Note 5 duration (s)	- -	0.037 0.001	0.067 0.031	- -	- -	- -
Number trills per call	- -	- -	3.03 0.15	3.96 0.30	- -	3.50 0.50
Number pulses per trill 1	- -	- -	2.94 0.08	4.38 0.27	- -	9.00 1.50
Number pulses per trill 2	- -	- -	4.30 0.10	4.16 0.21	- -	7.00 1.00
Number pulses per trill 3	- -	- -	4.41 0.14	4.37 0.25	- -	- -

Number pulses	-	-	5.05	5.10	-	-
per trill 4	-	-	0.12	0.12	-	-
Trill 1 duration	-	-	0.095	0.139	-	0.192
(s)	-	-	0.003	0.008	-	0.024
Trill 2 duration	-	-	0.125	0.117	-	0.172
(s)	-	-	0.003	0.005	-	0.044
Trill 3 duration	-	-	0.138	0.128	-	0.235
(s)	-	-	0.004	0.006	-	0.061
Trill 4 duration	-	-	0.141	0.143	-	-
(s)	-	-	0.005	0.007	-	-
Trill 5 duration	-	-	0.147	0.150	-	-
(s)	-	-	0.007	0.008	-	-
Trill 6 duration	-	-	0.167	0.155	-	-
(s)	-	-	0.010	0.013	-	-
Lower dominant	541	607	547	468	972	-
frequency (KHz)	86	21	20	14	102	-
Higher dominant	1227	1586	1541	1553	1667	-
frequency (KHz)	50	29	24	31	96	-
Sound pressure	70.4	66.5	68.9	70.4	-	-
level (dB)	0.3	0.3	0.2	0.3	-	-
N	2	71	96	22	16	2

Abbreviations: B=boink, S=series, SG=series growl, G=growl, C=cut, RG=release growl, M=mean, SE=standard error of the mean

Appendix B

DESCRIPTIONS OF STUDY SITES

1) Bog D, Hubbard County: A small (approx 125 sq m) body of open water surrounded by floating bog located at SE1/4 SE1/4 NW1/4 section 30, T143N, R35W.

2) Deming Lake, Hubbard County: A medium sized (approx 360 sq m) lake surrounded by mesic deciduous forest typical of the region located at SW1/4 SW1/4 section 30, T143N, R35W.

3) Enclosure site, Clearwater County: A medium sized (approx 100 m of shoreline) bay on the east shore of Lake Itasca. Adjacent to mesic deciduous forest. This site was where an enclosure was constructed to facilitate observation of mink frog social interactions and is located at SW1/4 SE1/4 SE1/4 section 2, T143N, R36W.

4) East Twin Lake, Hubbard County: A medium sized (approx 300 sq. m) lake surrounded by floating bog located at SW1/4 NE1/4 SW1/4 section 30, T143N, R35W.

5) Floating Bog Bay, Clearwater County: A large (approx 800 m of shoreline) bay on Lake Itasca bound by floating bog

and choked with wild rice (Zizania aquatica) located at SE1/4 NE1/4 section 11, T143N, R36W.

6) French Creek Bay, Clearwater County: A large (approx 550 m of shoreline) bay on Lake Itasca bound by floating bog, choked by wild rice, and located at S1/2 SW1/4 section 2, T143N, R36W.

7) Schoolcraft Island, Clearwater County: The only island on Lake Itasca. In past studies the mink frog was found most abundantly along approximately 80 m of the northwest shoreline of the island. This portion of the island is bound by floating bog and choked with wild rice. It is located at NE1/4 NW1/4 section 11, T143N, R36W.

8) South Deming Pond, Hubbard County: A small (approx 100 sq m) body of water surrounded by mesic deciduous forest located at NE1/4 SW1/4 section 30, T143N, R35W.

9) South Entrance Pond, Hubbard County: A medium sized (approx 250 sq m) body of water surrounded by floating bog and located at NE1/4 SE1/4 section 31, T143N, R35W.

10) South French Creek Bay, Clearwater County: A medium sized bay (approx 300 m of shoreline) surrounded by floating bog and choked with wild rice. Located at NW1/4 NW1/4 NW1/4 section 11, T143N, R36W.

11) West Arm Bay, Clearwater County: A small (approx 300 m of shoreline) bay on Lake Itasca surrounded by mesic deciduous forest and floating bog. Choked with wild rice and located at NE1/4 SE1/4 section, 15, T143N, R36W.

12) West Twin Lake, Hubbard County: A medium sized (approx 125 sq. m) surrounded by floating bog located at SW1/4 NW1/4 section 30, T143N, R35W.

LITERATURE CITED

Allan, D.M. Some relationships of vocalizations to behavior in the Pacific treefrog, Hyla regilla. Herpetologica 29:366-371; 1973.

Altmann, J. Observational study of behavior: sampling methods. Behaviour 49 (3,4):227-265; 1974.

Anonymous. Where have all the frogs gone? Modern Med. 41:20-24; 1973.

Arak, A. Vocal interactions, call matching, and territoriality in a Sri Lankan treefrog, Philautus leucorhinus (Rhacophoridae). Anim. Behav. 31:292-302; 1983.

Aronson, L.R. The sexual behavior of anura: IV. Oviposition in the mink frog, Rana septentrionalis Baird. Amer. Midl. Natur. 29:242-244; 1943.

Baird, D.; Eldridge, J.; Wiste, J. Notes on the territoriality and individual vocalizations of the mink frog (Rana septentrionalis). Univ. Minn. Forest. Biol. Stn. Paper 772. Lake Itasca, MN; 1972. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Berven, K.A. Mate choice in the wood frog, Rana sylvatica. Evolution 35(4):707-722; 1981.

Blair, F.W. Amphibians and reptiles. Sebeok, T.A. ed. Animal communication: techniques of study and results of research. Bloomington, IN: Indiana Univ. Press; 1968:293-300.

Bogert, C.M. The influence of sound on the behavior of amphibians and reptiles. Lanyon, W.E.; Tavolga, W.W. eds. Washington, DC: Amer. Inst. Biol. Sci. Publ. No. 7; 1960:137-320

Breckenridge, W.S. Reptiles and amphibians of Minnesota. Minneapolis, MN: Univ. Minn. Press; 1944.

Brzoska, J.; Obert, H. Acoustic signals influencing hormone production of the testes in the grass frog. J. Comp. Physiol. 140:25-29; 1980.

Caponi, C.R. Behavioral study of a population of male mink frogs (Rana septentrionalis Baird) making up a breeding chorus on Lake Itasca, Minnesota. Univ. Minn. Forest. Bio. Stn. Paper # unknown. Lake Univ. Minn., MN; 1976. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Capranica, R.R. The vocal repertoire of the bullfrog (Rana catesbiana). Behaviour 31:302-325; 1968.

_____. The auditory system. Lofts, B. ed. Physiology of the amphibia, vol. 3. New York, NY: Academic Press, Inc.; 1976:443-462.

Carroll, P.A. A study of the movements and vocalizations of a population of mink frogs (Rana septentrionalis) on the west arm of Lake Itasca. Univ. Minn. Forest. Biol. Stn. Paper # unknown. Lake Itasca, MN; 1976. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Case, S.M. Biochemical systematics of members of the genus Rana native to western North America. Syst. Zool. 27:299-311; 1978.

Cooke, A.S. Indications of recent changes in status in the British Isles of the frog (Rana temporaria) and the toad (Bufo bufo). J. Zool. Lond. 167:161-178; 1972.

Emerson, H.; Norris, C. "Red-leg"--an infectious disease of frogs. J. Exp. Med. 7:32-58; 1905.

Emlen, S.T. Territoriality in the bullfrog, Rana catesbiana. Copeia 1968(2):240-243; 1968.

_____. Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1:283-313; 1976.

Emlen, S.T.; Oring, L.W. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223; 1977.

Gerhardt, H.C. Mating call recognition in the green treefrog (Hyla cinerea): importance of two frequency bands as a function of sound pressure level. J. Comp. Physiol. 144:9-16; 1981.

Hedeen, S.E. The ecology and life history of the mink frog, Rana septentrionalis, Baird. Minneapolis, MN: Univ. Minn.; 1970. Dissertation.

_____. Growth of the tadpoles of the mink frog, Rana septentrionalis. Herpetologica 27:160-165; 1971.

_____. Postmetamorphic growth and reproduction of the mink frog, Rana septentrionalis Baird. Copeia 1972(1):169-175; 1972a.

_____. Escape behavior and cause of death of the mink frog, Rana septentrionalis. Herpetologica 28:261-262; 1972b.

_____. Rana septentrionalis. Zweiful, R.G. ed. Catalogue of American amphibians and reptiles. Athens, Ohio: Ohio Univ.; 1977: 202.1-202.2.

Hine, R.L.; Les, B.L.; Hellmich, B.F. Leopard frog populations and mortality in Wisconsin, 1974-76. Wisc. Dept. Natur. Res. Report 122; 1981.

Hird, D.W.; Diesch, S.L.; McKinnel, R.G.; Gorham, E.; Martin, F.B.; Kurtz, S.W.; Dubrovlny, C. Aeromonas hydrophila in wild-caught frogs and tadpoles (Rana pipiens) in Minnesota. Lab. Anim. Sci. 31(2):166-169; 1981.

Howard, R.D. Evolution of mating strategies in bullfrogs, Rana catesbiana. Evolution 32(4):850-871; 1978a.

_____. The influence of male-defended oviposition sites on early embryo mortality in bullfrogs. Ecology 59(4):789-798; 1978b.

_____. Mating behavior and mating success in wood frogs, Rana sylvatica. Anim. Behav. 28:705-716; 1980.

_____. Sexual dimorphism in bullfrogs. Ecology 62(2):303-310; 1981.

Kelling, S.T. Analysis of mating behavior, territorial behavior, and vocalizations of the mink frog, Rana septentrionalis, on Lake Itasca. Univ. Minn. Forest. Biol. Stn. Paper # unknown. Lake Itasca, MN; 1976. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Lemmerman, R.; White, O.; Life history and population study of the mink frog Rana septentrionalis- Baird on Schoolcraft Island. Univ. Minn. Forest. Biol. Stn. Paper 87. Lake Itasca, MN; 1958. On file at the Univ. Min. Forest. Biol. Stn., Lake Itasca, MN.

Lewis, R. Analysis of spacing characteristics and related phenomena in the mink frog, Rana septentrionalis. Univ. Minn. Forest. Biol. Stn. Paper # unknown. Lake Itasca, MN; 1972. On file at the Univ. Minn. Forest. Biol. Stn., La Lake Itasca, MN.

Marshall, W.H.; Buell, M.F. A study of the occurrence of amphibians in relation to a bog succession, Itasca State Park, Minnesota. Ecology 36:381-387; 1955.

Martof, B. Factors influencing size and composition of populations of Rana clamitans. Amer. Midl. Natur. 56(1):224-245; 1956.

MacDonald, J.; Engebretson, C. Life history, population and breeding readiness study of the mink frog (Rana septentrionalis) on Schoolcraft Island. Univ. Minn. Forest. Biol. Stn. Paper 140. Lake Itasca, MN; 1959. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

McKee, J.R. Morphological changes in ovaries and oviducts during the breeding season of Rana septentrionalis Baird. Univ. Minn. Forest. Biol. Stn. Paper 357. Lake Itasca, MN; 1962. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

McKenzie, D.S. A further study of the mink frog (Rana septentrionalis Baird) population on Schoolcraft Island. Univ. Minn. Forest. Biol. Stn. Paper 211. Lake Itasca, MN; 1962. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Merrell, D.J. A comparison of estimated and "effective size" of breeding populations of the leopard frog, Rana pipiens. Evolution 22(2):274-283; 1968.

_____. Life history of the leopard frog, Rana pipiens in Minnesota. Occasional paper-Univ. Minn. Bell Mus. Nat. Hist. 1977; 23 pp. Occasional paper no. 15. Avaialable from: Univ. Minn., Minneapolis, MN.

McKinnell R.G.; Gorham, E.; Martin, F.B.; Schaad IV, J.W. Reduced prevalence of the Lucke renal adenocarcinoma in populations of Rana pipiens in Minnesota. J. N. C. I. 63(3):821-824; 1979.

Moore, J.A. Patterns of evolution in the genus Rana. Jepsen, G.L.; Mayr, E.; Simpson, G.G. eds. Genetics, paleontology, and evolution. Princeton, New Jersey; Princeton Univ. Press; 1949: 315-338.

Narins. P.M. Effects of masking noise on evoked calling in a Puerto Rican coqui (Anura: Leptodactylidae). J. Comp. Physiol. 147:439-446; 1982.

Narins, P.M.; Capranica, R.R. Sexual differences in the auditory system of the tree frog Eleutherodactylus coqui. Science 192:378-380; 1976.

Odendaal, F.J.; Bull, C.M. The vocabulary of calls of Ranidella riparia (Anura: Leptodactylidae). Copeia 1983(2):534-537; 1983.

Peacock, B.; Drake, B. Notes on the bio-acoustic behavior of the mink frog (Rana septentrionalis Baird) at Lake Itasca, Minnesota. Univ. Minn.Forest. Biol. Stn. Paper 746. Lake Itasca, MN; 1971. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Priemer, L.C.; Strand, F.C.; Wichmann, A.K. Spacial arrangements, homing, aggression, and notes on amplexus in the mink frog, Rana septentrionalis. Univ. Minn. Forest. Biol. Stn. Paper 765. Lake Itasca, MN; 1973. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.

Ramer, J.D.; Jenssen, T.A.; Hurst, C.J. Size-related variation in the advertisement call of Rana clamitans (Anura:Ranidae), and its effect on conspecific males. Copeia 1983 (1):141-155; 1983.

Rand, A.S.; Ryan, M.J. The adaptive significance of a complex vocal repertiore in a neotropical frog. Z. Tierpsychol. 57:209-214; 1981.

Ryan, M.J. The reproductive behavior of the bullfrog (Rana catesbiana). Copeia 1980(1):108-114; 1980.

Salthe, S. N.; Mecham, J.S. Reproductive and courtship patterns. Lofts, B. ed. Physiology of the amphibia. New York, NY: Academic Press; 1974.

SAS Institute. SAS user's guide: basics. Cary, NC: SAS Inst. Inc.; 1982a.

SAS Institute. SAS user's guide: statistics. Cary, NC: SAS Inst. Inc.; 1982b.

Schmid, W.D. Some aspects of water economies of nine species of amphibians. Ecology 46(3):261-269; 1965.

Schmidt, R. S. Preoptic activation of frog mating behavior. Behaviour 30:239-257; 1968.

Seber, G.A.F. The estimation of animal abundance and related parameters. Griffin, London: 506 pp.; 1973.

Siegel, S. Nonparametric statistics for the behavioral sciences. New York, NY: McGraw-Hill Book Co.; 1956.

Wells, K.D. Social behavior of anuran amphibians. Anim. Behav. 25:666-693; 1977a.

_____. Territoriality and male mating success in the green frog, Rana clamitans. Ecology 58:750-762; 1977b.

_____. The courtship of frogs. Taylor, D.H.; Guttman, S.I. eds. The reproductive biology of amphibians. New York, NY: Plenum Publ. Corp.; 1977c: 233-262.

_____. Territoriality in the green frog (Rana clamitans): vocalization and agonistic behavior. Anim. Behav. 26(4):1051-1063; 1978.

Wiewandt, T. Vocalization, aggressive behavior, and territoriality in the bullfrog, Rana catesbiana. Copeia 1969(2):276-285; 1969.

Wright, A.H.; Wright, A.A. Handbook of the frogs and toads of the United States and Canada. Ithaca, NY: Comstock Publ. Co.; 1949.

Wunderle, J.; Wenstrom, B. Some notes on the breeding behavior of the mink frog (Rana septentrionalis Baird) at Lake Itasca, Minnesota. Univ. Minn. Forest, Biol. Stn. Paper 755. Lake Itasca, MN; 1970. On file at the Univ. Minn. Forest. Biol. Stn., Lake Itasca, MN.